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THE MOLECULE IN BIOLOGICAL STRUCTURES AS DETERMINED BY X-RAY METHODS

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THE intimate structure of organized bodies has been for a long time a fascinating field for speculation among biologists, especially among those who are interested in growth and functions of living organisms. It was thought that knowledge of this nature would make clearer an understanding of the mechanisms of vital processes. Nägeli's attempts (1) in 1858 were among the first to explain properties of biological structures by means of a molecular hypothesis, although he preferred to think in terms of molecular aggregates which he called micelles, particles composed of several thousand molecules. His conceptions based on growth, swelling and optical phenomena have stimulated investigations along many lines, even up to the present day; however, it was not until the first of the present century that the micelle became a physical reality. This was due to the invention of the ultramicroscope. The molecule and the atom remained for the most part "convenient mental abstractions having no actual existence," until about twenty years ago. At that time, to the physicist at least, they became actual particles with fairly definite structures and properties. The demonstration of their existence did not come as a surprise to many physicists and chemists, for numerous investigations had already strongly indicated their reality, which, however, awaited the brilliant work of Laue and his colleagues (2) for confirmation. They were able, by making use of crystals as diffraction gratings for X-rays, not only to show that atoms and molecules were physical entities, but also to open new fields for investigation in many branches of science; and as a result, physicists and chemists at the present time seem far more satisfied with their conceptions of molecules than are many biologists with their notions concerning centrosomes, mitochondria, genes and filtrable viruses. In spite of the fact that molecules are far below visibility with the most powerful microscope, for the smallest visible particle may be a thousand or more large molecules in diameter, it is possible by means of X-ray crystal structure methods to measure these minute entities with a considerable degree of accuracy, and in many cases to show the relative position

of their component atoms. From this information it is now possible to make models of molecules, built to scale, large enough for more leisurely study; and since the molecule as a unit of structure is more simple than the biological cell as a unit, there seems to be a possibility of gaining a somewhat clearer comprehension of the living organism through studies of these models.

As mentioned above, X-radiation is involved in these investigations. Its value for biological investigations in a somewhat different capacity was recognized almost immediately upon its discovery, made by Roentgen in 1895, for a radiation which would allow a visual examination to be made of the bones in a living body was of too great importance to be overlooked by the surgeon. At first it was thought that the rays had no ill effects on the body; but it was not long before serious flesh burns were found to be caused by this new radiation, and with this discovery a new property of X-rays came forcibly to the attention of the biologist. These two properties, penetration of opaque materials, and injury to living tissues, held the attention of the biologist for nearly three decades. During that time the physicist was studying the X-rays themselves, and was finding them to be a prolific source of information concerning the atom and the structure of matter. Through his discoveries a third field was opened up to the biological investigator, that of studying physically the molecular structure of plant and of animal tissues. Research in this field has not developed very far up to the present time, principally because the technique is complicated and demands a training involving phases of physics and chemistry for which biologists in general do not seem to feel the need. Nevertheless, the work seems important enough to warrant a review, in which an attempt is made to show, in a fairly simple way, the methods and processes involved in these molecular studies, and to give a brief account of some of the results obtained.

Each of the three fields of investigation mentioned is associated primarily with a particular characteristic of X-radiation, and for that reason, some of the properties of X-rays are mentioned here briefly, merely to recall them to mind (3, 4). In attempting to characterize X-rays in a few words, it may be said that they are electromagnetic waves of very short wave-length. The size of the wave-length makes possible the shadow photographs of the surgeon; the electromagnetic nature of the radiation is associated with the effect upon living matter; and the characteristics of the waves as such are brought into direct use in molecular structure investigation. Of course, the characteristics of waves are not to be considered as completely separate from the electromagnetic effects, nor from wave-length, but the apparent predominance of one characteristic over the others has resulted in three types of investigation each having its own particular technique.

We may think of a beam of X-rays as consisting of waves of many different wave-lengths ranging from approximately 0.2 Ångström unit (an Ångström unit is 10^{-8} cm. or $\frac{1}{10,000,000}$ mm.) to about 2.0 Å, as opposed to visible light, in which the wave-lengths are several thousand times as long. Due to its short wave-length X-radiation is enabled to penetrate opaque substances. The shorter the wave-length, the "harder" the ray is said to be, and the greater is its penetrating power. On the other hand the "soft" ray is of longer wave-length and does not penetrate so deeply. The power of penetration varies not only with the wave-length but also with the substance. In other

words, the penetrating rays are absorbed to a greater extent in one substance than in another. It is due to this ability of X-rays to penetrate substances, and in addition, to the ability of the substances to absorb the rays differentially, that shadow pictures of one substance embedded in another are made possible. The well known photographs of bones and teeth are examples of such pictures.

The electromagnetic nature of X-ray waves leads one to anticipate disturbances of some kind in the minute electrical systems of the component atoms and molecules of substances, when they are irradiated. Such disturbances might well be expected to occur in active protoplasm, where metabolic reactions are so nearly balanced. One may think of these reactions as occurring in some orderly fashion, and when a disturbance is produced, the routine of the reactions may be changed, resulting in new structural or other developments. Practically nothing of the nature of these disturbances is understood, and a molecular picture of the mechanisms which are involved in X-ray burns, and in mutations in genetical investigations, is at present decidedly vague; but in spite of that, the work that is being carried on in these fields, while necessarily empirical, seems to be yielding rich returns. The situations involved, however, are of such great complexity that a clear understanding of the reactions seems to be a matter of the distant future.

The wave properties of X-radiation and the minute size of its wave-lengths are characteristics which have made X-rays a powerful tool with which to investigate the structure of matter. Direct evidence has been obtained of the existence of atomic and molecular entities. The investigations have shown that the atom occupies space corresponding to a sphere of about 1.5 Å to 2.5 Å in diameter, and that the size of the atom for a given element is fairly constant, varying only slightly in different types of molecules. Investigations (4) have brought out the concept of the molecule as a group of atoms which are held strongly together into a single entity; and considerable information has been obtained concerning the relation of molecules spatially to one another, the distances which separate them, their sizes, shapes and orientations. Still further, with the help of data from sources other than X-rays, it has been possible to determine the arrangement of the atoms within the molecule itself. In practically all cases, solid crystalline materials were employed for investigation; relatively very little work has been done on liquids and colloidal systems.

The methods used to demonstrate these facts concerning molecular structure were based upon physical and crystallographic theories, and brought together the wave theory of light, the lattice theories of crystal structure, and more commonly known physical and chemical laws. The procedure in these investigations is an outgrowth of the early successful attempts of Laue, Friedrich and Knipping in 1912 to use a crystal as a diffraction grating for X-rays (2); and of the work in the same year of Sir William Bragg and W. L. Bragg in simplifying the method (4).

The importance attached to these discoveries is indicated by the great number of investigations reported since that time (3); hundreds of crystals have been examined and their "fine" structure, that is, their atomic or molecular structure, determined. By far the greater number of these reports has dealt with inorganic crystals and metals; only relatively few organic crystals and a still smaller number of biological structures have been investigated. The work done on organic crystals is of direct, although of secondary in-

terest to the biologist since it is through the structure of the individual organic crystal that a knowledge of the existence of the individual molecule as an entity is obtained.

In 1923 it was shown that, in all probability, in the benzene crystal the six-carbon benzene ring represented the unit of structure (5) just as the individual brick in a brick wall is the unit. Shortly thereafter, in the carbohydrates, the six-carbon group was shown also to be the unit (6), and in fatty acid crystals the long hydrocarbon chain proved likewise to be a structural entity (7). The methods used were found to be applicable to biological materials; and when applied to the solid components of organisms, especially those parts which seemed to be layered in structure, they have given noteworthy results. Among structures of this type cellulose, as found in the wall of plant cells, has been perhaps the one most extensively investigated, although a dozen or more biological substances have been examined. A list of such substances includes starch grains, chitinous plates, tunicin, hair, wool, feathers, quills, muscle tissue, hemicelluloses, and a few structures such as bone, dentine, eggshell, etc. Substances which might be classified as by-products of metabolism or as being associated in some less direct way with the organism, such as rubber, gelatin, and glue have also received more or less attention.

Before attempting to give the results obtained by various investigators in their work with the substances just mentioned, a description of the procedure used in determining the molecular structure of these materials by X-ray analysis is presented. No attempt is being made to describe the work in all of its details; instead, it is hoped that the discussion will bring out the underlying principles and in the end give a picture of the molecule whenever the investigations have proceeded far enough. Concepts of X-ray physics, crystallography, and organic chemistry are involved, and it is likely that the terminology of these three fields may creep into the discussion; however, the effort is being made to make the descriptions intelligible to those who are not familiar with the jargon of one or another of these specialized branches of science. Minute exactness will undoubtedly suffer at the expense of more readily attained conceptions, but should the details be desired, it is hoped that the references cited will either provide the information or will lead to references which will furnish it. The literature is so extensive that only references which seem to be essential are given.

The experimental methods and the procedure which were used in interpreting the data for the various steps employed in determining the structure of cellulose, are taken here as more or less illustrative examples of the work done on biological materials in general, since they embody certain details of technique which are likely to be applicable to other organized structures.

In the studies of cellulose many kinds of plant cells were examined but the fiber was found to be the type best suited for intensive study. Bast fibers of ramie, *Boehmeria nivea*, have proved more useful than have other fibers such as tracheids of wood, hairs of cotton or bast-fibers of flax and hemp; these, however, have the same molecular structure.

The problem at hand, then, is to obtain a conception or picture of the molecules of cellulose, and of their arrangement in the wall of a fiber. The picture is built up bit by bit from the interpretations of experimental data obtained primarily through X-ray crystal structure methods (8). With suitable apparatus records, usually photographic, were obtained of beams of X-rays

which had been reflected from layers of atoms occurring in the wall of the fiber. Interpretation of these records made it possible to construct a geometric model showing the arrangement of the molecules. In order to make clear the method of obtaining the photographic data and of interpreting the latter, the various steps in the process will be taken up under several headings which will be seen to lead progressively to a conception of the molecular structure.

A great deal of the work is associated with a fundamental relationship which exists between three things: the X-rays, the angle at which the beam impinges on the fibers, and the distance between the layers of atoms in the fiber. Three quantities are involved in this relationship, the wave-length of the X-ray waves, which is designated as λ; the angle, θ, at which the beam glances off from the layers of atoms in the fibers; and the distance, d, which separates the layers of atoms. The relationship is expressed by the Bragg formula,

$$\lambda = 2d \sin \theta$$

It is possible to determine the value of λ and θ; therefore the value of d, the distance between the atomic layers, is merely a matter of computation.

When the values of d for a number of sets of atomic layers in the fiber have been determined, it then becomes necessary to obtain the positions of these layers relative to one another. This constitutes the second step.

From this information it is possible to construct a picture of the molecular lattice, from which the elementary cell and the molecular unit of structure are determined.

As the fourth step, a model of the unit of structure is fitted to the lattice; thereupon the picture of the molecular structure of the fiber wall begins to take shape.

The position of the lattice as it occurs in the fiber relative to the long axis of the fiber and to a tangential and a radial orientation in the fiber, will be taken up for consideration as the final step.

DETERMINATION OF ATOMIC LAYERS

The determination of d the distance between atomic layers in the various sets of layers occurring in the fiber, is essentially experimental. The apparatus employed is so constructed that the X-ray beam will have a known wave-length, λ, and that the value of the glancing angle, θ, may be determined.

In its simplest form the apparatus may be represented by the diagram in Fig. 1,

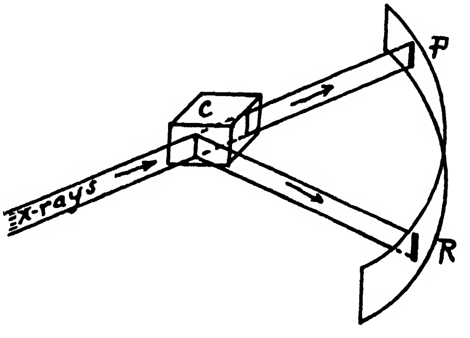


Fig. 1. Perspective Diagram to Show Beam of X-rays Passing Through Crystal, C, to Photographic Film at P; and Beam from Crystal Reflected to the Film at R

where, for convenience of explanation, a simple crystal has been substituted for the fibers at C. When a beam of X-rays from a narrow slit is allowed to impinge on the face of the crystal at C, the beam is split into two beams; one passes on straight through the crystal to the curved photographic film at P, the other is diffracted, or for simplicity of conception let us call it reflected, from the crystal to the film at R. Upon development of the film two black lines appear. One was made by the principal beam; the other, by the reflected beam.

The reflected beam is produced only

when the body at C is built up of many layers of atoms. The layers must be parallel to one another and equally spaced. In the figure they are presumed to be parallel also to the face of the crystal. As the beam penetrates the crystal it passes through many of these layers, but not all of it is able to pass, for each layer reflects a small amount, and when the beam impinges on the layers at a certain definite angle these small amounts reinforce one another and produce the line at R.

As mentioned above, a definite relation was shown by Bragg (4) to exist between the *angle* at which the beam impinges on the layers, indicated by θ in Fig. 2; and the *distance* which separates layer from layer, which was designated as d; and the *wave-length*, λ, of the X-ray waves, such that $\lambda = 2d \sin \theta$. The significance of the two black lines on the film will now become apparent, for from them it is possible to determine the angle θ. In Fig. 2, which is a plan view of Fig. 1, the angle, θ, made by the face of the crystal and the impinging beam is the same as that made by the reflected beam, OR, and also, by the principal beam OP, with the crystal. The distance from P to R on the film then measures the arc of 2θ. By construction of the film holder, O is made the center of the arc PR and the radius of OP is definitely fixed and is a known value. With the arc and the radius known, the value of $\sin \theta$ is merely a matter of computation. Thus one value for the equation above is determined.

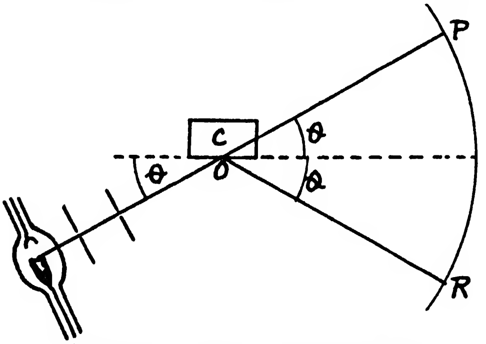


Fig. 2. Diagram to Show Relation of Angle θ to the Principal and Reflected Beams of Fig. 1

The relationship indicated by the equation $\lambda = 2d \sin \theta$, holds only when the X-ray beam consists of waves of a single wave-length; that is, when the beam is monochromatic. It is an easy matter to obtain a beam of this kind, and further, a beam in which the wave-length λ has a known value. This will be discussed later. With λ known, the only unknown in the equation is d, the distance between the planes or layers of atoms; and when d is computed we shall know several things about the body at C. It must have many layers of atoms arranged parallel to one another and all uniformly spaced with the distance between them equal to the value of d as computed from the equation.

If we turn the crystal at C around so that the layers parallel to another face are in reflecting position, the angle, θ, for that face may be found to have a different value, and d, therefore, would also have a different value for this new set of planes or layers. By reflections from other faces the interplanar values of several sets of planes may be determined. If now the angles between these various faces are measured, we shall have the necessary data from which to build a large scale model of the *layers* of the crystal. We cannot build the model from solid planes but if we place blocks at the *intersections* of the planes we shall have a structure in which the planes are all evident, but each plane will consist of a layer of the blocks instead of being a solid layer. This may be seen in Fig. 3 which is a photograph of such a model.

The older theories (9) concerning the structure of a crystal demanded a lattice of elementary particles. We have represented those particles by the blocks in Fig.

3 and the whole structure may be called a three dimensional lattice or, more commonly, a space lattice. The blocks or points of the lattice are known to be identical with atoms or clusters of atoms. The cluster may be a whole molecule, several molecules, or only a part of a molecule. In any case, the distance between the layers is the *d* of the equation.

At this point it may be desirable to consider briefly the quality of the X-ray beam (4) for we are interested here in the use of a monochromatic beam. If the beam as indicated in Figs. 1 and 2 were an

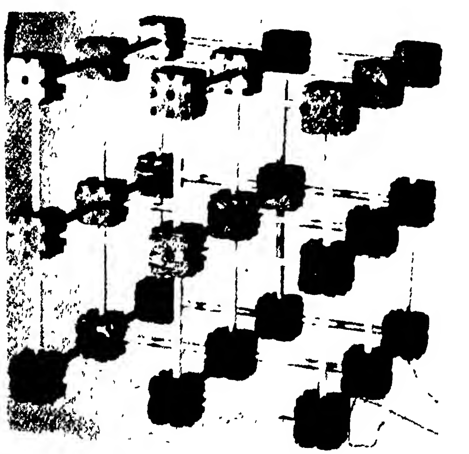


FIG. 3. MODEL OF A SPACE LATTICE WITH BLOCKS AT THE INTERSECTIONS OF THE PLANES

unaltered beam of full strength from an X-ray tube, it would be composed of waves of many different wave-lengths, just as ordinary daylight consists of waves of many sizes. When, in the latter case, the wave-lengths are sorted out by a prism into a spectrum they range in size from about 3900 Å at the violet end to about 7700 Å at the red end. In a somewhat similar manner the wave-lengths of an unaltered X-ray beam, or of "white light" as it is sometimes called, may also be sorted out. These are found to be several thousand times shorter. At one end of the spectrum the wave-lengths may be less than 0.2 Å and at the other end, nearly ten times that length. The distribution of the different wave-lengths in the beam may be nearly uniform, as in ordinary sunlight where no single color or wave-length predominates. This situation exists in the X-ray beam when low voltages are applied to the tube, but when the voltage is stepped up considerably, a single wave-length increases greatly in excess of the others. More specifically, the beam from a molybdenum tube excited at 20,000 volts will have a somewhat uniform distribution of wave-lengths; but, at 40,000 volts, waves of 0.7 Å wave-lengths will occur far in excess of all others; somewhat comparable to a beam of daylight mixed with an intense monochromatic beam such as green light. In both cases it is possible to filter, or screen out, all but the dominating color or wave-length, and thus to obtain a monochromatic beam. In the X-ray beam the predominating wave-length at high voltages is different and characteristic for each element used as a target in the X-ray tube; for tungsten it is 0.21 Å; for molybdenum, 0.71; for copper, 1.54 Å. The exciting voltage differs also for each. To utilize these characteristic wave-lengths practically all others may be screened out by using specific metallic screens; for example, a zirconium filter for a molybdenum target, and one of nickel for the copper radiation.

Returning for a moment to Figs. 1 and 2 and to the equation, $\lambda = 2\,d \sin\theta$, it will be noticed that in the equation, λ refers to a specific wave-length. Obviously then in using an apparatus designed as indicated by the figures, the X-ray beam must be passed through a screen to make it monochromatic. Tubes are readily obtainable with molybdenum, tungsten or with copper anticathodes; and by using the proper screen, λ of the equation becomes a known quantity.

THE RELATIVE POSITIONS OF ATOMIC LAYERS

In practice the procedure is somewhat more complicated than that implied in the description above of work with a single simple crystal, for in biological structures the molecular arrangement is not at all likely to be that of a simple crystal. In the latter the crystal faces are readily seen and the investigator may determine by ordinary crystallographic methods, the faces which are likely to be most advantageous for reflection. But, with biological structures, it is not possible to determine crystal faces by the usual methods;

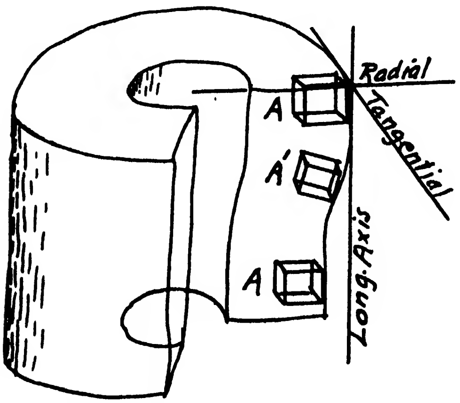


Fig. 4. Greatly Enlarged Piece of Fiber with a Sector Cut Out of It
Possible axial lines are indicated

as a rule, they have no faces that have any resemblance whatever to crystal faces. In the case of ramie fibers which we are using here as an example of a biological structure, the fiber is in the form of a cylinder, very slender, perhaps fifty microns in diameter, and very long, often many centimeters in length. The only features of such a structure that even remotely resemble crystallographic axes are the long axis of the fiber, a radius of the cylinder and a line tangential to the surface of the fiber (see Fig. 4).

In order to apply the concepts of the crystal and of X-ray reflection described above, we may imagine a very small cubical piece of the wall, as *A* in Fig. 4, to replace the crystal in Figs. 1 and 2. The front face of that minute block is parallel to the surface of the fiber and the top face represents a transverse plane, across the fiber. Obviously there would be a very large number of these imaginary blocks similarly situated with respect to the surface and to the transverse planes in a fiber; and in order to have an amount of the fiber material sufficiently large, in the path of the beam, to produce reflections to the film a bundle of fibers about 3 mm. thick is required.

Of the hundreds of thousands of such blocks, then, in the path of the beam, a large number would be found to be oriented to exactly the right position to pro-

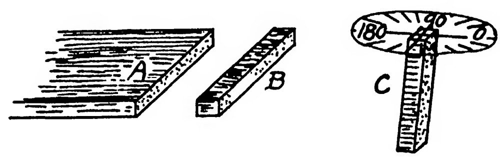


Fig. 5. Diagram to Represent Method of Holding Fibers for X-ray Exposures

duce a minute reflection from, say, the front face of each; that is, the face which is tangential to the fiber. Another large number would reflect from the side face, that is, a face radial in the fiber; and still another group would reflect from the transverse planes. Such is the case when the fibers are crumpled up and packed into a small 3 mm. pellet. Lines from all three faces of the block would appear at the same time on the film, under those conditions, since each block which was in the proper position for reflection would reflect its small quota to the film, where the summation of all of these small reflections would produce the respective lines. But if the fibers were laid parallel in a bundle, then evidently the *transverse* planes of most of them could be made to form the proper

angle with the beam, all at the same time, and a very strong line would be produced, while practically none of the radial and tangential planes would then be in position to reflect, since the angle θ is a small angle of only a few degrees.

A glance at Fig. 5 may make this somewhat clearer. It represents a convenient device for controlling the position of the fibers. Long fibers were laid parallel and cemented with collodion into a rectangular bundle about 3 mm. thick, 15 mm. wide and of indefinite length, as indicated at *A*. A small piece, *B*, was cut off and attached to a circular protractor as shown at *C*. 5.15 Å. From this we are enabled to say that there were many *transverse* planes, or layers, of atoms in the fibers, all spaced 5.15 Å from each other and that these planes were at right angles to the long axis of the fiber. A microtome cross-section of the fiber, one micron thick, might represent a stack of about 2000 of these flat washer-like atomic layers.

If now the protractor is rotated through a quarter of the circle, all of the fibers will lie lengthwise in the beam, along the line 0°–180°, and planes of atoms which extend *lengthwise* of the fiber will be in position to reflect the beam to the film; while the transverse planes will have been turned out of the reflecting position. Here, however, a situation occurs, somewhat different from the preceding and from that in crystals in general, but similar in many respects to the condition found in almost all biological structures, for the cylindrical or curved nature of the material demands special consideration.

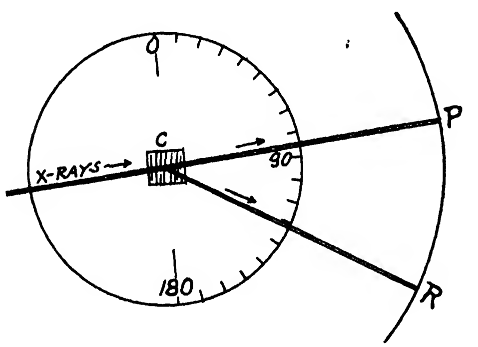


Fig. 6. Block of Fibers, Attached to Protractor, Placed in Position for X-ray Exposure

Letters as in Fig. 2. Fibers indicated at nearly right angles to beam.

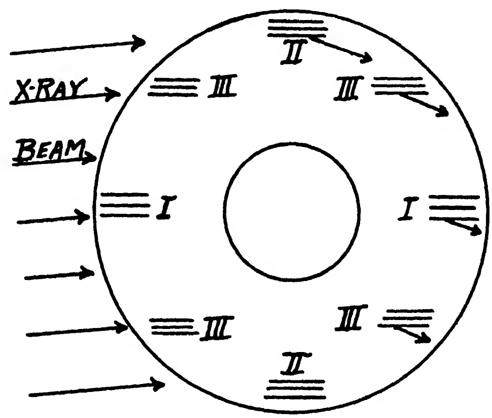


Fig. 7. Cross Section of Fiber with Positions of Reflecting Planes Indicated I, II, III

Thousands of 3 mm. lengths of fibers, of which the piece was composed, would then lie parallel to one another (8), and when the device was placed in the position of the crystal as shown in Fig. 6, it could be rotated so that the beam would pass through at right angles to the long axis of all the fibers in its path. In this position the transverse planes would reflect to *R* on the film, from which, when developed, the distance from *P* to *R* would be a measure of the arc of 2θ for the transverse planes in the fiber.

When this value of θ was used in the formula, $\lambda = 2d \sin\theta$, d was found to be

When the X-ray beam passes lengthwise through the fiber it finds radial planes, as at I in Fig. 7, and tangential planes as at II, both in reflecting positions, and if those planes have different values for d,

two reflected beams will appear on the film. The photograph taken from that position showed two lines representing planes spaced 6.10 Å and 5.40 Å respectively. We may now say that, in addition to the planes of atoms which extend across the fiber, there are also planes which extend lengthwise. They may be radial and tangential planes respectively, but this is not so conclusive as that the planes considered above are transverse, for if they were in some diagonal position as at III, Fig. 7, they would also produce a reflected line.

The problem, however, is not quite so simple and the whole story has not been told for either of the two positions of the protractor. The photographs obtained from them contained lines other than those mentioned and still more lines were obtained when the protractor was turned to positions lying between 0° and 90°. At the 0° mark a strong line from planes spaced 3.98 Å appeared accompanying the 6.10 and 5.40 lines, as shown in the reproduction of the photograph in Fig. 8. From the 90° position several more lines appeared in addition to the 5.15 line. These are also shown in Fig. 8. When the protractor was turned to the 10° mark, the photograph showed two new lines produced by planes which were not quite parallel to the long axis of the fibers. At the 20° mark other new planes were brought into active reflecting positions; at 30° still more new lines were produced

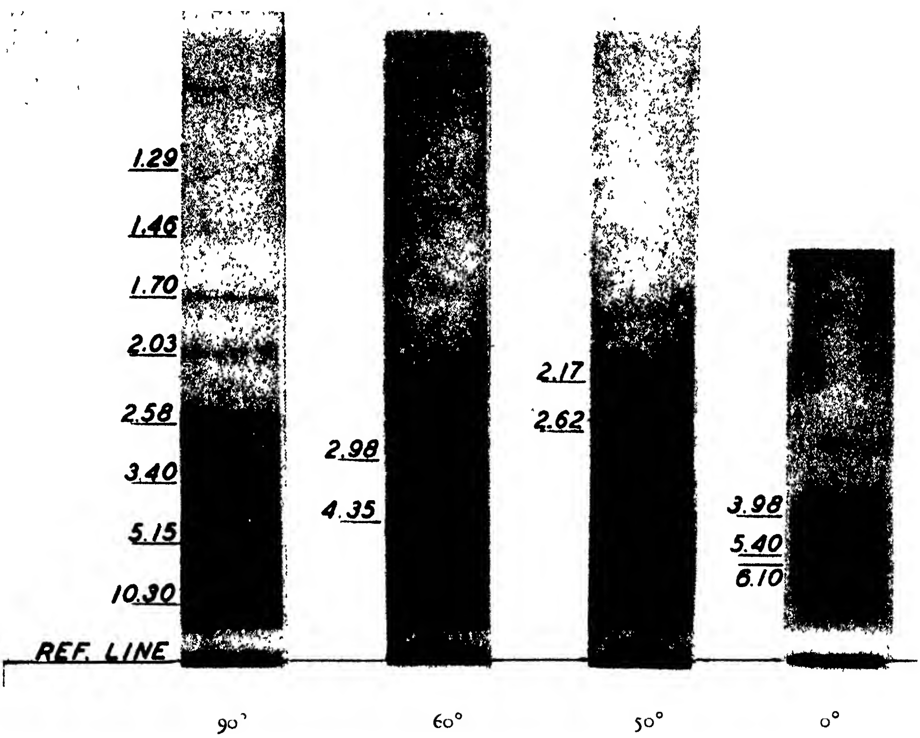


Fig. 8. Reproduction of Photographic Films Showing the Lines Reflected from Fibers
Position of fibers indicated by 0°, 90°, etc., which refer to protractor readings (see Fig. 6). Interplanar spacings for the lines are given opposite the respective lines.

on the photograph and so on for each ten degree interval to the 90° mark. In all more than thirty lines were found.

THE MOLECULAR LATTICE

Only a few of these lines will be considered here, although all of them must be accounted for in the finally accepted lattice. The former will be used to demonstrate the methods for determining the relative positions, in the lattice, of the planes which produced them; and to show how the molecular structure is deduced from the relation of these planes to one another. In order to help make this clear Fig. 3 is revised, as shown in Fig. 9, to

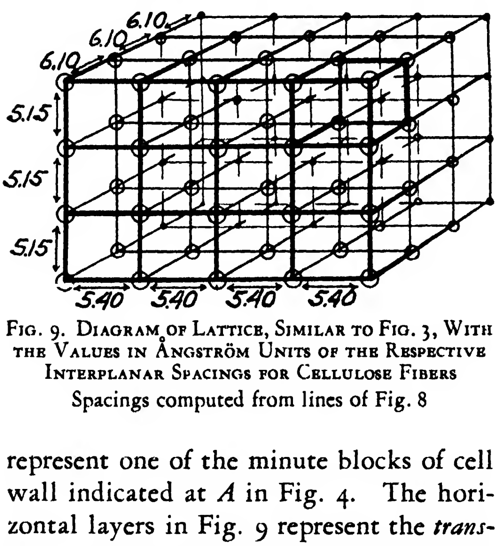


FIG. 9. DIAGRAM OF LATTICE, SIMILAR TO FIG. 3, WITH THE VALUES IN ÅNGSTRÖM UNITS OF THE RESPECTIVE INTERPLANAR SPACINGS FOR CELLULOSE FIBERS
Spacings computed from lines of Fig. 8

represent one of the minute blocks of cell wall indicated at *A* in Fig. 4. The horizontal layers in Fig. 9 represent the *transverse* atomic layers which our photograph from the 90° position of the fibers showed to be spaced 5.15 Å. The layers parallel to the front face of the same block we will assume are spaced 6.10 Å, and those parallel to the sides, 5.40 Å. These two sets of layers we know, from the 0° position photographs, extend *lengthwise* of the fibers. But since we do not know the relation of these two layers or planes to each other, our assumption for the moment is merely a guess.

In the fiber, this minute block (Fig. 9) would appear somewhat as in Fig. 10, where a piece of the fiber is shown in a perspective diagram, but enormously out of proportion relative to the lattice. Another assumption is made here, that the 6.10 Å layers are *tangential* and the 5.40 Å layers are *radial* in the fiber. The validity of this assumption also will be discussed later. In the figures, the small black circles represent reflecting units of some kind which occur at the intersections of the planes, and of which the planes themselves are composed. These units forming the space lattice in the fiber are spaced 6.10 Å, 5.40 Å, and 5.15 Å respec-

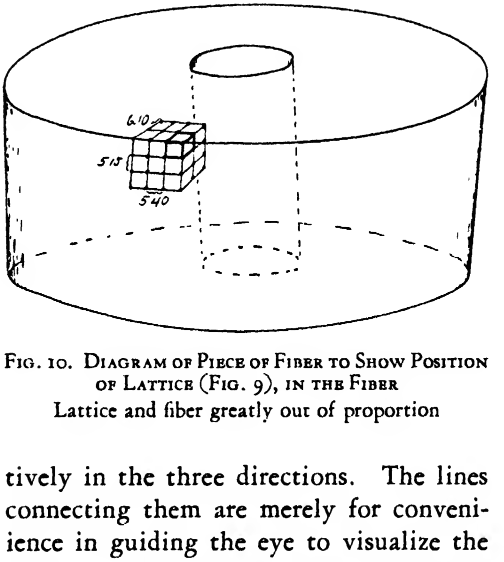


FIG. 10. DIAGRAM OF PIECE OF FIBER TO SHOW POSITION OF LATTICE (FIG. 9), IN THE FIBER
Lattice and fiber greatly out of proportion

tively in the three directions. The lines connecting them are merely for convenience in guiding the eye to visualize the layers. The lattice, then, may be thought of as composed of cells which are 6.10 x 5.40 x 5.15 Ångströms in size. These are spoken of as the elementary cells of the lattice (3,4). One is shown in Fig. 11 and also one in the near corner of Fig. 9. It is obvious that the elementary cell may be used to represent the whole block of cell wall referred to in Figs, 3, 4, 9 and 10, and that any layers which occur in the block must also occur in the elementary cell. The layers which outline the cell, the faces of the cell, are of

course not the only layers or planes associated with it. Many diagonal planes are distinguishable such as *BCHE*, *DCFE* and *ACGE*, to mention only three of them. Each one represents a great number of planes in the fiber, parallel to it and all uniformly spaced. For example, *BCHE* has a plane parallel to it passing through

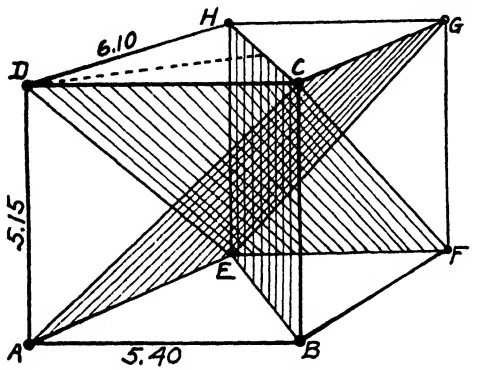


FIG. 11. SINGLE ELEMENTARY CELL OF LATTICE TO SHOW RELATIVE POSITIONS OF VARIOUS PLANES

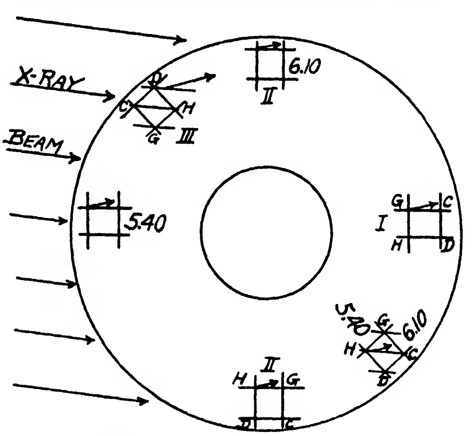


FIG. 12. CROSS SECTION OF FIBER TO SHOW POSITION OF PLANES WHICH WERE INDICATED IN FIG. 11

AD, also another one through *FG*. The *distance*, *d*, between these planes is the perpendicular distance from *D* to the line *CH* (shown by a dotted line), and this distance may be computed since we know that *DC* is 5.40 Å and *DH* is 6.10 Å, provided that we know also the angle between those two sets of planes. Further, when we look back to Fig. 7 and revise it as in Fig. 12, where only the top layer of the elementary cell is shown at the positions of I, II, and III of Fig. 7, it may be seen that at I, in Fig. 12, the planes which are spaced 5.40 Å will be in position to reflect the beam; at II, the 6.10 planes will reflect, and at III the *diagonal* plane which passes through *CH* of the cell should also reflect the beam. We might expect then to find on the photograph which shows the 5.40 and 6.10 lines, another line from planes which are spaced a distance equal to the dotted line from *D* to *CH* in Fig. 11. On the photograph in Fig. 8, 0° position,

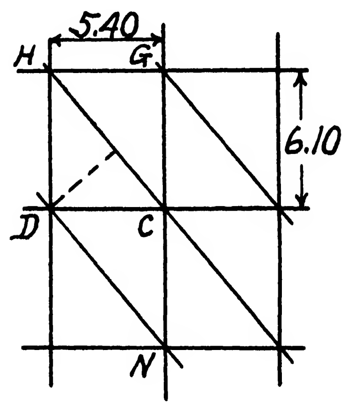


FIG. 13. FOR EXPLANATION SEE TEXT

a third very strong line is shown. It is produced by planes spaced 3.98 Å. If we assume that the 6.10 and 5.40 planes form right angles as in Fig. 13, then the diagonal planes, represented by *CH* and *DN*, are separated by the distance from *D* to the plane *CH* which, when computed, is found to be about 4.05 Å. The experimentally determined 3.98 is close enough to the theoretical value 4.05 to serve as a first approximation. Therefore, for the moment, we may accept the elementary cell as being an orthorhombic structure (3); that is, one in which the angles between the faces are right angles. This is a tentative working hypothesis which

will be checked by other diagonals and modified to fit them, since the structure which is finally accepted must have planes corresponding to all of the lines found on the photographs.

The set of diagonal planes with the interplanar spacing of 3.98 Å produced an exceptionally strong line; that is, strong relatively to the 6.10 and 5.40 lines. This indicates that the atoms associated with the corners *B*, *C*, *H*, and *E* of Fig. 11 are located in positions which are more efficient as a group in reflecting from the diagonal planes, as represented by *BCHE*, than from the face planes of the cell; that is, from the 6.10 and 5.40 planes. The question then arises, what atoms or molecules may we expect to find at these corners?

THE MOLECULAR UNIT

The chemist assures us that cellulose consists of only three kinds of atoms: carbon, hydrogen and oxygen. A conception of the elementary cell with only one atom at each corner is not consistent either with the intensities of the lines on the X-ray photographs or with the sizes of the atoms (3), which incidentally have radii of less than one-fourth the distance from corner to corner of the cell. It seems more reasonable then to think that a *group* rather than a single atom occurs at each corner. The most obvious group for consideration is that composed of six carbon, ten hydrogen and five oxygen atoms, ($C_6H_{10}O_5$), since it contains, in simplest numbers, the proportion of each of the elements, in cellulose. If this group, which is called a glucose residue, occupies a space equivalent to the volume of the elementary cell or bears some integral relation to it, there would be a high degree of probability that the group is the structural unit.

The volume of the $C_6H_{10}O_5$ group may be computed from data which are in no way associated with the X-ray data from cellulose. It is known that there are 6.062×10^{23} molecules in a gram-molecule of a substance. In the case of cellulose the $C_6H_{10}O_5$ group may be accepted as the molecule for this purpose. Its molecular weight is 162. The gram-molecule, 162 grams, then contains 6.062×10^{23} glucose groups. The volume of 162 grams of cellulose is 103.2 cubic centimeters since the specific gravity is 1.57; that is, one cubic centimeter weighs 1.57 grams. If then 6.062×10^{23} groups occupy a volume of 103.2 cubic centimeters, the volume of

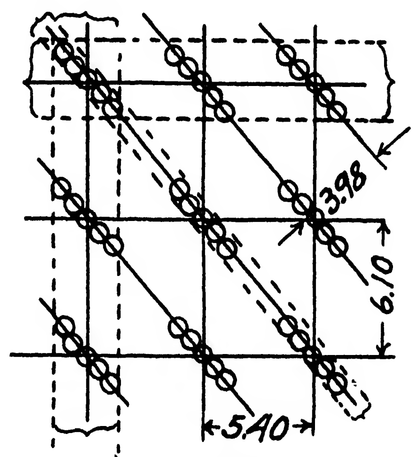


Fig. 14. Diagram to Indicate Molecular Groups in the Lattice and Molecular Layers or Planes

one group is $103.2 \div 6.062 \times 10^{23}$ which is 170×10^{-24} cc. or 170 cubic Ångströms. Returning now to our tentative elementary cell, we find its volume $6.10 \times 5.40 \times 5.15$ to be 169 cubic Ångströms. The agreement between these two volumes, elementary cell 169, glucose residue group 170, makes it seem very probable that the group of atoms located at the corner of the elementary cell is identical with the $C_6H_{10}O_5$ group of the chemist.

Attention was called to the exceptionally strong 3.98 line in Fig. 8. The significance of this becomes clearer now when we revise Fig. 13 by placing $C_6H_{10}O_5$

groups at the corners of the cells in Fig. 14. When they are so placed that most of the atoms lie along the diagonal planes and close to it, they form a relatively thin layer of atoms from which the 3.98 lines are produced; while at the same time in the direction of the 6.10 and 5.40 planes they form thick layers as indicated by the dotted lines. Since all of the atoms of a given set of layers are effective in reflection, the intensity of the line produced is in this case dependent to a great extent upon the thickness of the individual layers in some inverse ratio (3). The arrangement of the atoms in the group seems to fit, at least qualitatively, the density of the lines shown in Fig. 8. For a more complete demonstration of this the literature (10) may be consulted.

A molecular picture of the fiber is now beginning to be unfolded. Figure 14 might represent a view of the molecular arrangement on a cross-section of the fiber. It is quite impracticable to draw a complete cross-section of a fiber to scale and show the molecular arrangement, for if the layers of molecules were represented by circles only $\frac{1}{8}$ inch in diameter, it would require a circle 400 feet in diameter to represent the fiber cross-section. Referring again to fig. 14, we have shown up to this point, that if we could magnify a *cross-section* of a fiber sufficiently and could attune our eyes to see individual molecules we would perceive an orderly arrangement as in the figure, with the distances from center to center as indicated, and the molecules would appear longer along one diagonal than in any other direction.

We now turn to the appearance of the groups as seen on a tangential or radial section of the fiber; and elect, as a convenient angle at which to view them, to look along a line such as the dotted line in Fig. 13 from *D* to *CH*. This will give a broadside view of the $C_6H_{10}O_5$ group. When the fiber block of Figs. 5 and 6 was rotated to the 90° position several lines (Fig. 8) from transverse planes in the fiber were produced in addition to the 5.15 line which was used in the tentative elementary cell. These additional lines indicate the presence of *several sets* of atomic planes *all* parallel to one another and *all* at right angles to the long axis of the fiber. The interplanar spacings corresponding to the more prominent lines are 5.15 Å; 3.40; 2.58; 1.70; 1.29. If a small sub-group of atoms existed half-way between the 5.15 planes,

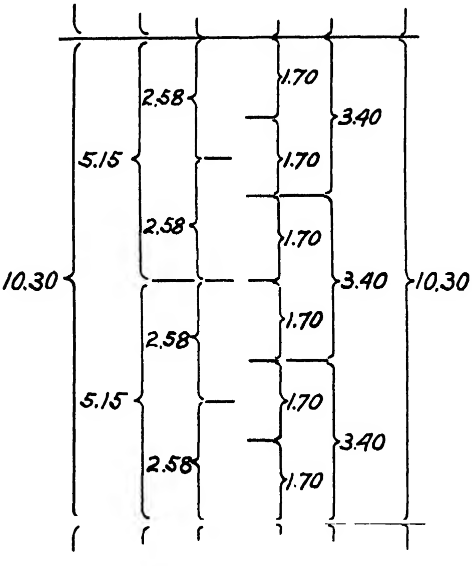


FIG. 15. FOR EXPLANATION SEE TEXT

it would account for the 2.58 line; and if another sub-group interleaved the 2.58 planes, the 1.29 line would be explained; but 3.40 does not seem to bear a multiple relation to 5.15. If, however, we were to consider *two* of the glucose groups as forming *one* structural unit, the total length of which is 2 x 5.15 = 10.30 then all of the lines would be accounted for. This double unit, 10.30 Å long, repeated lengthwise of the fiber, may be more clearly understood from Fig. 15, where the multiple relation between the various planes is brought out.

The combined effect of reflections from all of the atoms within each 10.30 distance produces a resultant line on the photographic film; the resultant for all within the 5.15 distances produces another line; for all within 2.58 distances still another line, and so on. It would seem then that with these interleaved groups spaced so closely together, the glucose *units* would not appear to be so distinctly separated in the lengthwise direction of the fiber, as they are in the transverse view. They would have the appearance of chain-like structures extending lengthwise of the fiber parallel to one another with the chains spaced 6.10 Å in one direction and 5.40 Å in another (11). The groups in Fig. 14 would represent the end view of these chains as seen on the transverse section of the fiber.

Up to this point, we have considered only the lines which were produced by transverse layers and by layers which extend lengthwise of the fiber. These lines were obtained from exposures with the fibers in the 90° and 0° positions respectively (Fig. 8). The remaining twenty odd lines represent diagonal layers and were produced by rotating the fibers to positions between 0° and 90°. In the geometrical figure which was finally accepted as representing the lattice, diagonal planes were found which corresponded to all of these lines.

Returning again to a consideration of the individual chain, we must now think of every 10.30 Å length of it as being exactly like the next adjoining 10.30 Å length along the chain; and of the unit of structure along the chain as consisting of two $C_6H_{10}O_5$ groups, each 5.15 Å long. In order to explain the 10.30 and 3.40 lines on the film, we must suppose one of the two groups to be oriented slightly differently from the other; the chain then consisting of a single row of $C_6H_{10}O_5$ groups, with the alternate groups alike in orientation.

The elementary cell must now be revised to include this new conception of two groups forming the unit distance along the chain. The revision merely makes two of our former elementary cells into one twice as long; that is, 6.10 x 5.40 x 10.30. But when we examine the reflection lines obtained from the block of fibers at positions between 0° and 90° (Fig. 5), we find that in order to explain the occurrence and intensities of some of them we must alter again the dimensions of the elementary cell. This time it is due to a difference in orientation of one *whole chain*

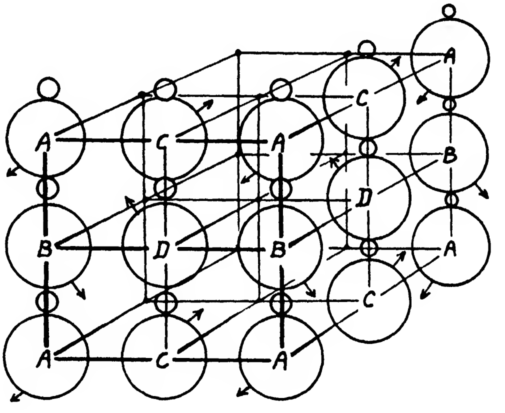


Fig. 16. Diagram to Show Molecule of the Lattice Oriented to Four Different Positions, Indicated by A, B, C, and D

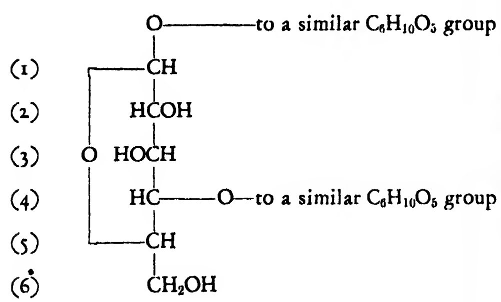
Large circles represent the glucose residue; the small circles, the oxygen bridges. Arrows merely indicate different orientations.

from that of the next adjacent chain; thus *alternate chains* in the 6.10 and 5.40 layers are so rotated on their long axis that the alternate *chains* have like orientation, otherwise all of the chains are alike. This construction, with the chain consisting of a single row of $C_6H_{10}O_5$ groups, all alike chemically, but with only the alternate ones oriented alike in the chain, and the *chains* also all alike except that only the alternate chains have like orientation, accounts for all of the thirty-odd lines obtained in the X-ray diffraction patterns. In Fig. 16 a diagram of this

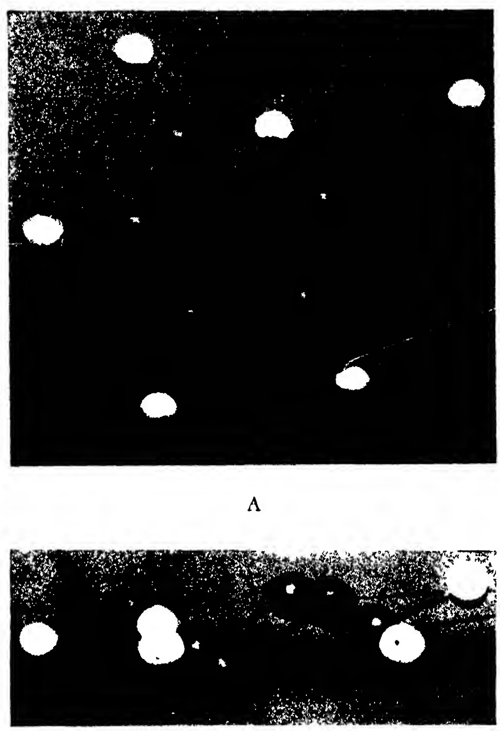
arrangement is given. The large circles which represent whole $C_6H_{10}O_5$ groups now replace the black dots of Figs. 3 and 9. In the latter case the dots represented merely the centers of some kind of reflecting units, now we may substitute a $C_6H_{10}O_5$ group for each reflecting unit. The letters, *A*, *B*, *C*, and *D*, in the figure, are used to indicate the difference in orientation of the glucose groups. Those of a given letter have like orientation. The arrows are used merely to help that conception.

ATOMIC MODEL OF THE UNIT OF STRUCTURE

The chemist, through his experimental methods, gives us the relation of the atoms to one another in the molecule and indicates the structure of cellulose somewhat like this:



When, however, we use the physicist's dimensions of the atoms concerned (3), the picture of the group becomes a three-dimensional structure of a very different shape. The four valence bonds of the carbon atom are localized at tetrahedral positions on each atom; that is, at positions which would correspond to alternate corners of a cube, about 109° apart (12). The two bonds of the oxygen atom are also at tetrahedral points (13). The distances from center to center of the atoms are generally accepted as about 1.50 Å, carbon to carbon; and 1.40 Å, carbon to oxygen. The hydrogen atoms may be ignored since their contribution to X-ray reflection here is not measurable. In constructing a model, however, the diameter was considered to be roughly about 1 Å. A photograph of a three-dimensional model using these dimensions and angles is shown in Fig. 17 a and b. When carbon 1 is attached through an oxygen atom to carbon 5, a ring structure is formed which



A

B

Fig. 17. Reproduction of a Three-dimensional Model of a Glucose Molecule; A, Flat View, B, Edge View

Black spheres represent carbon atoms; white, oxygen. Hydrogen atoms are not shown.

turns out to be 5.15 Å long; that is, from the oxygen atom of carbon 1 to the oxygen atom of carbon 4. According to the chemist, these two oxygen atoms act as bridges which link the glucose residues or groups together by primary valence forces into long chains; and when the adjacent residues are oriented slightly differently, but

with the alternate ones all alike, the structure is in agreement with the elementary cell constructed from the X-ray diffraction patterns (10, 14). It is interesting to note that, at the same time this lattice model was being worked out by the author from X-ray data, chemical evidence was presented independently for the same ring structure (15), and for the same oxygen bridge as was used in the arrangement of residues in the chain.

In Fig. 18 the relation is shown between the various sets of planes and the atoms in the model. In our first attempt at fitting

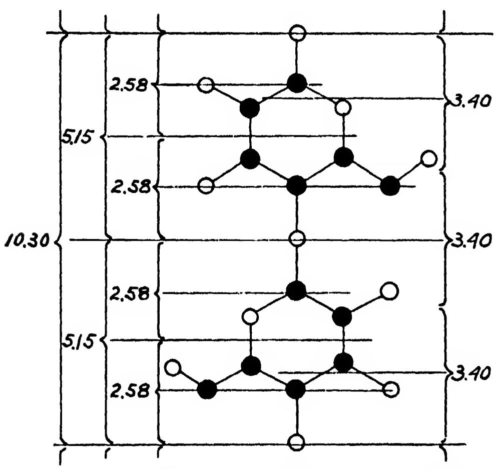


Fig. 18. Diagram to Show Relation of Model to X-ray Data

the model to the lattice we placed the residues with C_4 attached to C_4, and C_1 to C_1 (8). Since then more chemical evidence has been produced which strongly indicates a C_1 to C_4 linkage (16). Either arrangement may be made to fit the model, but a discussion of this point is of little importance at the present time to the biologist. Another phase of orientation is, however, of more direct interest; that is, the position not merely of one of the units or one of the chains, but of the *whole lattice* as it occurs in the wall with respect to the fiber as a whole.

POSITION OF LATTICE IN FIBER

In Fig. 14, where the end view of the chains is shown, they are indicated as being flattened along one of the diagonals. The model fits very well into this arrangement both in shape and in dimensions. But whether the *lattice* is so arranged that a certain set of planes is always tangential to the surface of the fiber, as we have tentatively assumed in Figs. 10 and 12, or whether it has some other arrangement, does not appear from the data presented up to this point. In a cylindrical structure such as a fiber, the different sets of planes which lie parallel to the long axis, will be found to lie all at the same time, in a position favorable for reflection somewhere in the fiber, as shown by Fig. 7. There seems to be no way of determining

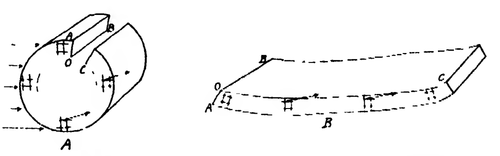


Fig. 19. A, Piece of Fiber Split Lengthwise; B, Same Piece Flattened Out, to Show Position of Lattice

directly their position with respect to one another, or to the surface of the cylinder; but if the cylinder could be split lengthwise and flattened out as indicated in Fig. 19 then each set of planes could be brought into reflecting position independently of the others, and then by rotating through known angles, the relative positions could be determined. Obviously, however, the fibers are too small to be split, and besides, some thousands would have to be piled up into a block, in order to have enough material to produce a diffraction pattern. In searching for other material which could be used in this way, the large cells of a seaweed, *Valonia*, were found to be satisfactory (17, 18). They are spherical cells 10 to 20 mm. in diameter. Pieces

group for a given organized substance will have little value.

It seems doubtful whether any structure of plant or animal origin will be found, which will yield to structural analysis with the same degree of assurance of accuracy that is possible with inorganic crystals, or even with organic crystals. In any case the fine structure of a material should offer a reasonable explanation for many *properties* of that material; and whenever an exact determination cannot be arrived at with the certainty that is obtained for many inorganic crystals, the relation of the structure to its properties is a reasonable source of information upon which to draw. For example, in the studies on cellulose the molecular lattice was worked out with only one assumption of a chemical nature. That assumption was that the molecular unit is identical with the glucose residue which is obtained from cellulose upon degradation by hydrolysis. But, in order to fit this residue into the lattice, it was necessary to turn to carbohydrate chemistry for the basic evidence bearing on the positions of the atoms in the glucose molecule (10). That evidence showed that the residues were linked through an oxygen bridge, while the X-ray data pointed to the long chain, with the residues forming links of the chain. Additional chemical evidence has lately been presented (20) to support this conception of chains of indefinite length. To the same end, investigations by X-rays on many derivative products of cellulose (21) have shown that the 5.15 Å distance, which is the length of the residue, remains as predicted (10), wherever the fibers are not broken down in the process. From another point of view, physical properties of the fiber are in agreement with the chain structure. The coefficients of thermal expansion (22) indicate that lateral vibration is greater than longitudinal; and swelling experiments (23) show that the chains separate laterally, while no extension longitudinally takes place. Both are in accord with the lattice proposed, where primary valence forces hold the units into the chain more strongly than the forces known as van der Waals' forces hold the chains together laterally.

The development of the glucose-residue chain conception of the structure of cellulose was the outgrowth of a number of investigations covering a period of nearly two decades. As the work progressed, the methods and technique changed somewhat, resulting in greater accuracy in determination of the lattice. In 1913, shortly after the discovery of the use of crystals as diffraction gratings for X-rays, two Japanese investigators reported (24) X-ray evidence of molecular uniformity in the structure of fibrous materials. After an interval of seven or eight years, several reports appeared in German periodicals (25), in which the dimensions of the elementary cell of a lattice were given, but the data were insufficient for a detailed picture of the cellulose structure. A few years later, 1925–1926, three articles (8, 10, 11) appeared in American journals embodying the essentials of the structure as described in the present paper. In 1928 several German investigators (16) verified this structure with only a slight alteration, that of the orientation of the alternate glucose residues in the chain. This change was made in order to bring the structure into better agreement with chemical evidence which was then available. Since then X-ray work with cellulose has dealt mainly with its properties, and with its derivatives. The measurements of a dozen or more derivatives in which the fiber retained its gross structure, show that the 5.15 Å unit distance, the length of the glucose residue, is retained throughout (21).

The methods of crystal analysis have

been improved somewhat during the past decade, although the fundamental principles have remained the same. Two of these modifications may be of especial interest to the biologist; the first is a method of *obtaining the reflections* of X-rays from the materials, the second is a means of *determining the reflecting planes* of the lattice. Concerning the former, instead of using a slit to control the X-ray beam, a minute round hole is used. The beam from this pin-hole is allowed to pass through the material under investigation and the reflected beams are recorded on a

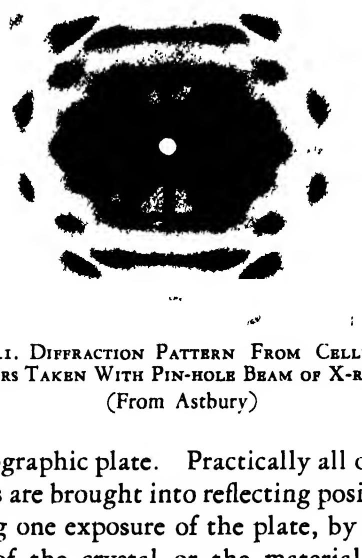


FIG. 21. DIFFRACTION PATTERN FROM CELLULOSE FIBERS TAKEN WITH PIN-HOLE BEAM OF X-RAYS (From Astbury)

photographic plate. Practically all of the planes are brought into reflecting position, during one exposure of the plate, by rotation of the crystal or the material (3). Fig. 21 is a reproduction of such an exposure of cellulose fibers. Each spot is the result of reflection from a specific set of atomic planes.

A simple means of determining the planes, in crystallographic terms, from these spots was devised (26) in the form of a chart. Fig. 27 is an example of the use of the chart, where the spots from X-ray patterns of hair and wool have been transferred directly from the photographic films. The reflecting planes for each spot may be read directly from the chart and in most cases a far greater degree of certainty is obtained than was possible with the method described above. For details of the later method the reader is referred to the original report and to Wyckoff's "Structure of Crystals," New York, 1931 edition.

OTHER BIOLOGICAL STRUCTURES

As has been mentioned in the early part of this article, a dozen or more biological materials and structures in addition to those of cellulose have been studied by X-ray methods. Only a few of these have so far yielded results which may be considered as even moderately satisfactory for the interpretation of molecular structure. Numerous investigations of carbon compounds brought to light several outstanding points which are of especial interest to the biologist, since they are sufficiently fundamental to be applicable to studies of organized materials in general.

Through the work of several investigators (27) it has been shown that in the fatty acids the long hydrocarbon chain is a zig-zag structure. It corresponds to a structure built up of carbon atoms having diameters of 1.5 Å attached to each other at tetrahedral angles (109°), and as increasingly higher forms were studied, it was shown that the length is increased by a specific distance for each —CH_2— group added to the chain. The distance is slightly less than 1.3 Å, which is in good agreement with corresponding distances between the carbon atoms of the diamond (12). With this work in mind one feels greater confidence in accepting a similar zig-zag arrangement for the carbon atoms in the carbohydrates, and in fact, in the carbon compounds generally.

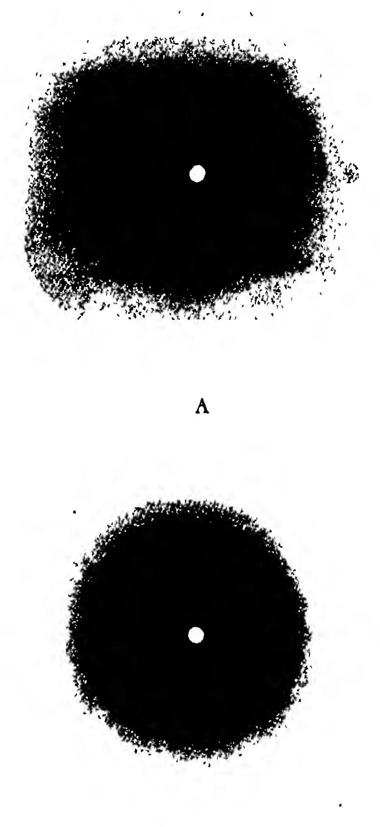
A great deal of emphasis has been placed upon the idea that organized substances are composed of long chain molecules (14).

To most of these substances, as will be seen in the following brief accounts, there has been assigned a molecular structure based primarily on analogy to cellulose either from the similarity of X-ray diagrams or from the similarity of chemical and physical properties. For none of these substances has there been as complete an X-ray analysis as for cellulose. In many cases such completeness may not be possible, but in others more concentrated work may give as good or better results.

There seems also to be a general assumption arising from the work on fiber structure, that "fibers are fibers, because their molecular components are fibrous;" and structures have been proposed upon that basis when sufficient X-ray data were not available for the purpose.

Rubber

When raw rubber is in a stretched condition, an X-ray pattern may be obtained from it; but when the rubber is in an unstretched condition the photograph is similar to that obtained from amorphous materials. The pattern from the former was interpreted as indicating the existence of long chain molecules in which isoprene groups are the units, somewhat as glucose groups are units in the cellulose chain. Isoprene (C_5H_8), from its formula, might be considered comparable to the hydrocarbon chain of the fatty acids in so far as the atomic arrangement in its molecule is concerned. This possibility was taken into consideration apparently, when the structure of rubber was proposed (14), for the X-ray pattern, Fig. 22, contains only a few lines. These lines alone were insufficient for the determination of the lattice, but with the help of data from chemical sources and from various other sources in which the physical properties of the rubber were concerned, the lattice was worked out. The two types of photographs obtained were interpreted as indicating that the stretching and the contraction of rubber were associated with a corresponding straightening out and wrinkling of the long chain molecules.



A

B

Fig. 22. X-ray Patterns from Rubber; A, When Stretched to Seven Times Its Original Length; B, Unstretched
(From Astbury)

Carbohydrates

In a somewhat similar manner, conceptions of the structures of several carbohydrates have been proposed, which were based to a great extent upon the chemical formulae, and only partially upon X-ray data supplemented by physical properties, and strengthened by analogy to the structure of cellulose. Among these are starch,

lignin and hemicelluloses, tunicin and chitin, and others. From none of these substances has an X-ray pattern been obtained which is sufficiently clear and which has enough detail to justify more than a tentative structure. Since most of the reports on carbohydrate investigations have been collected in a late publication in book form (14), we shall describe here only very briefly the molecular structures which have been proposed for them.

Hemicelluloses, such as occur in date seeds and the fruits of several palms, produce sharp X-ray patterns, but up to the present time no clear cut demonstration of the lattice has been offered. A chain structure has been proposed (14), in which hexose residues act as the units; however, it is based primarily upon chemical considerations.

Concerning lignin practically nothing has been determined by X-ray means, but from chemical considerations, again, a primary valence chain comparable to that in cellulose is thought to represent the structure (14).

The crystalline nature of the starch grain has been debated for nearly a century; but it was not until 1920, when X-ray diffraction patterns were reported (25), that the existence of a crystalline regularity of its atoms was definitely demonstrated. A few years later the molecular unit of structure was shown, with a fair degree of probability, to be a glucose residue (6). Soon after that, evidence was presented which made it seem probable that the arrangement of the units in the starch grain was not the same for grains from different kinds of plants (35). The structure has not yet been satisfactorily worked out, although from its chemical and various physical properties a chain structure similar to that of cellulose was proposed (14) in which glucose residues are the links of the chain.

The so-called animal cellulose, tunicin, which forms the framework of the tunicates is capable of producing a moderately good X-ray pattern, sufficiently good it was thought (14) to consider it as indicating a molecular chain structure identical with that of plant cellulose. Curiously its diffraction pattern is quite like the pattern which may be obtained from the alga *Valonia* in that its 6.08 Å and 5.45 Å planes correspond to the 6.10 Å and 5.33 Å planes respectively of the latter, and also in that the angles formed by these

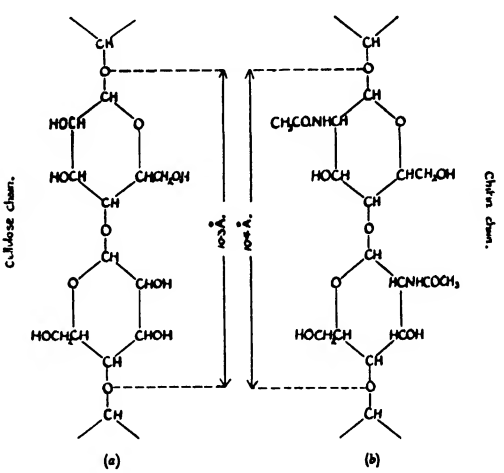


FIG. 23. DIAGRAM TO SHOW RELATION OF CHAIN MOLECULE OF CELLULOSE TO THAT OF CHITIN

planes are the same. Its diagonal, spaced 3.95 Å corresponds to the 3.93 Å of *Valonia* (28). That an animal such as a tunicate is capable of forming cellulose is in itself interesting, but that the cellulose is deposited in the same molecular arrangement as that in the plant cell wall is remarkable, and may have a special significance when the methods of deposition are more fully studied.

Chitin, as represented by the wing covers of the Goliath beetle, gave an X-ray pattern from which a repetition period of 10.4 Å was obtained (14). The similarity to the 10.3 period of cellulose led to a

proposed chain structure in which acetylglucoseamine residues with a ring structure almost identical with that of cellulose, acted as the links of the chain. Fig. 23 shows the similarity between molecules of the two substances. The principal difference is in the addition of an NHR group to carbon number two of the glucose residue. The evidence for this is entirely of a chemical nature.

Proteins

Of all structures built by organisms, those composed of proteins are undoubtedly of the greatest interest to the biologist; they are also the most elusive, as becomes obvious when one attempts to gain a conception of their structure. The large size and the great complexity of protein molecules make an understanding of their structure seem exceptionally difficult, if not hopelessly impossible to attain. The relation of amino acids to the proteins offers a certain amount of hope, however, and X-ray studies on silk, wool, hair and other proteinaceous fibers add further encouragement. In 1921, and also a year or so later, it was reported that such fibers (29) were capable of producing X-ray diffraction patterns which were similar to those of cellulose fibers, although less complete and less well defined.

In 1923, the idea was advanced (30) that silk-fibroin consisted, to a considerable extent, of primary valence chains arranged parallel in the direction of the fiber. The similarity of the X-ray pattern, Fig. 24, to that of cellulose, Fig. 21, indicated a long chain structure in the silk also. The elementary cell which was proposed showed that the chains were spaced 4.40 Å and 4.84 Å laterally at nearly right angles, while along the chain the repetition distance was given as 7.0 Å. It is this last dimension which is of especial importance in connection with proteins in general, for the conception was advanced that the chain consisted of peptide linkage units with the residues of the amino acids attached as side chains. In the silk fibroin the amino acids involved are principally glycine and alanine. When they are built

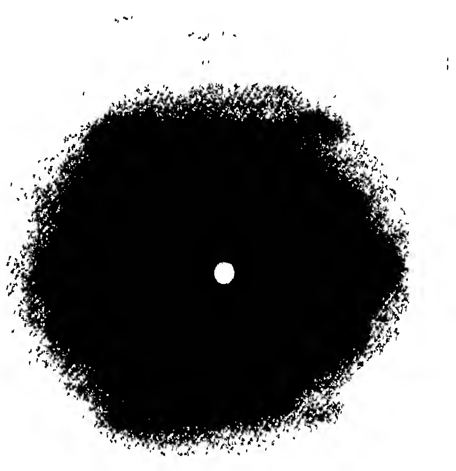


FIG. 24. X-RAY PATTERN FROM NATURAL SILK
(From Astbury)

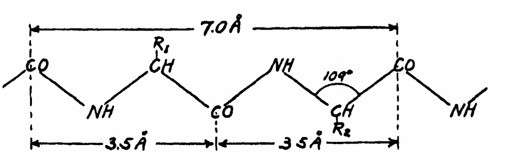


FIG. 25. DIAGRAM TO SHOW RELATION OF PEPTIDE LINKAGES TO X-RAY SPACINGS FROM SILK
(From Astbury)

to scale into a chain somewhat as in the diagram, Fig. 25, the distance from —CO— of the glycyl residue to —CO— of the alanyl residue was found to be about 3.5 Å; the total length for the two units, 7.0 Å, is the same as the repetition distance determined from the X-ray pattern of the silk fiber. A diagram of the model is shown

in Fig. 26. The structure is one which seems to be in harmony with various physical properties of the silk fibers, and may be considered as the most satisfactory one proposed up to the present time. A significant feature of it is that it provides a way for placing amino acids which vary in size into a chain, in which the links have a uniform length of about 3.5 Å along the fiber axis. The remaining part of the amino acid residue then becomes effective in governing the distance to which the chains may be separated. Another correlation which is of interest here

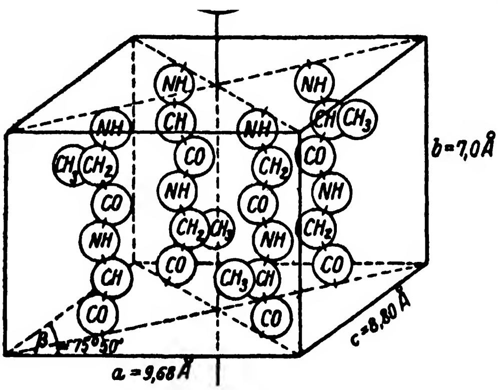


Fig. 26. Elementary Cell of Silk
(From Meyer and Mark)

is that the distance between four $—CH_2—$ groups in the fatty acid chain mentioned above, $—CH_2—CH_2—CH_2—CH_2—$, is practically the same, 3.7 Å, as that from one —CO— group to the next —CO— group, —CO—NH—CH—CO, of the peptide chain, 3.5 Å. The similarity in dimensions is at least striking.

A more marked advance was made on protein structure in 1930 when a group of investigators (31, 34) in England worked with human hair, wool, quills and feathers, all of which were found to give essentially the same X-ray pattern. From the type of the pattern, which was similar to that of cellulose, they felt that, in general, they were dealing with small units of structure, rather than with units as large as those indicated by the high molecular weight of the protein, keratin, the principal constituent. Two types of X-ray patterns were found, Fig. 27 a and b, one from stretched

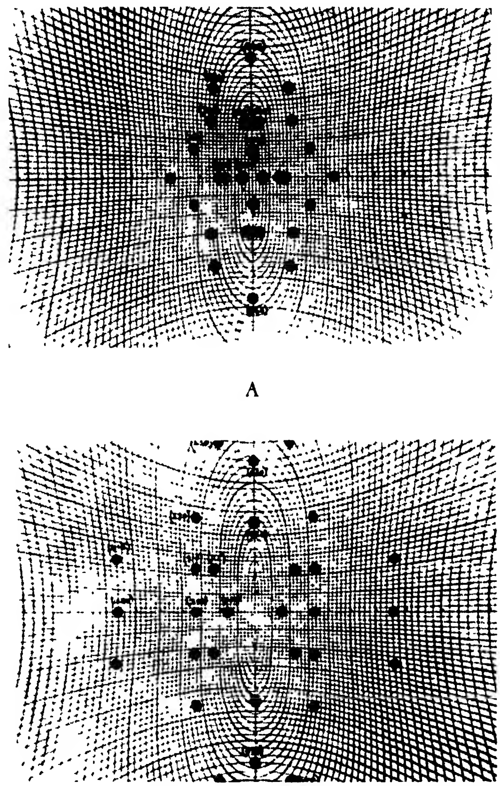


Fig. 27. Diffraction Patterns from Hair, Transferred to Bernal Charts; A, Unstretched; B, When Hair was Stretched to Double Its Original Length
(From Astbury)

hair, the other from hair in the normal unstretched condition. In both cases the patterns showed a definite repetition distance along the fiber axis; 5.15 Å for the normal condition and 3.4 Å for the stretched material. The pattern of the former gradually disappeared during the stretching process, and at the same time

the pattern of the stretched hair became more and more prominent until the extension had reached about 70 per cent of the original length, when the former had completely disappeared. Other changes in the X-ray patterns also occurred. Accompanying the change along the fiber axis, the two chief lateral spacings of 27 Å and 9.8 Å respectively of the normal hair gradually disappeared and narrower spacings, 4.65 Å and 9.8 Å replaced them in the stretched condition. These changes were interpreted as showing the unfolding of a long primary valence chain molecule making it thinner, and consequently drawing the chains closer together. The chain was considered as consisting of peptide linkage units as indicated above in connection with silk-fibroin, where the distance 3.5 Å between —CONH— units corresponded to 3.4 Å in the *stretched* hair; while the 5.15 Å distance of the normal hair corresponded to a folded condition as represented in Fig. 28. Wherever an R appears in the figure a residue of one of the several component amino acids is indicated. One of the 5.15 Å units represents three of the 3.4 Å peptide units when the hair is stretched. These interpretations were found to correspond quantitatively with the stretching measurements, and with other properties of hairs; and when taken altogether, they furnish a very reasonable picture of protein fibers. While it would be desirable to work with material which would give more clear cut X-ray diagrams, the present conception is acceptable until such material is forthcoming.

In addition to the proteinaceous materials already mentioned, other types have been examined by various investigators with the hope of finding one which would allow a more satisfactory X-ray analysis. Tendons, sinews and muscle tissues gave X-ray patterns but were far from satisfactory from the point of view of molecular structure; nevertheless they helped to build up a conception of the protein molecule. In a stretched condition, as opposed to a shrunken or contracted state, the change in pattern showed that there had been a rearrangement of particles of small molecular size, and when considered in connection with certain chemical and physical properties there seemed to be an indication here also of the existence of

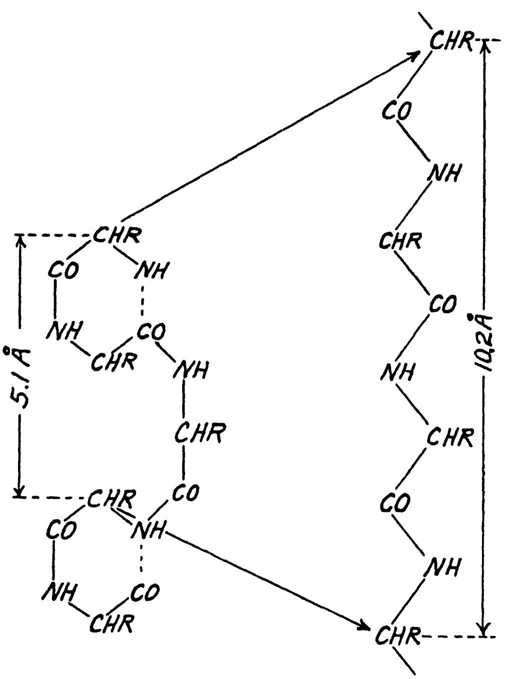


Fig. 28. Diagram to Show Relation of Folded Protein Molecule in Unstretched Hair (Left), to Stretched Molecule (Right)

long fibrous molecules (14). Further conclusions were for the most part speculative.

In summarizing the work done on structures which are built of protein materials, one feels no small degree of satisfaction in finding that the chemical units, amino acid residues, apparently remain intact as physical entities in the large protein molecule, or at least one may say that the evidence points very decidedly in that direction. Furthermore there seems to be

a definite interval which is repeated over and over in the length of the long protein molecule in spite of the fact that the units vary in size laterally, since each unit may be associated with a different kind of amino acid residue. The length of the interval fits well with the length of the three groups involved in a peptide linkage, thus allowing for the construction of a chain-like molecule of almost any length. The distance from chain to chain seems to be governed by the size of the

FIG. 29. X-RAY DIAGRAM FROM GELATIN
(From Clark)

amino acid residues which project out from the sides of the chain.

These conclusions apply to structures of more or less permanent shape, which have considerable tensile strength. Structures of this kind not only seem to have long chain fiber-like molecules in their composition, but also to have these chain molecules placed in parallel arrangement forming the larger fiber-like structures. Proteins occur in the organism, also, in a more mobile form, where one would scarcely expect to find a parallel arrangement of the long molecules. An approach to the study of materials of this nature has been made through the use of gelatins and glues (32, 14). Comparatively little work has been done with them, and that, probably, out of curiosity as to whether they were amorphous or crystalline rather than as an attempt to determine their fine structure. Under certain conditions they were found to produce wide rings on the photographic plate when a pin-hole beam of X-rays was passed through them. The rings resembled somewhat those produced by liquids in general, except for the fact that they were more clear cut. In Fig. 29 a reproduction of such rings from gelatin is given. They indicate a certain degree of regularity in the arrangement of the molecules, suggesting the presence of minute pseudo-crystalline particles in random arrangement.

MICELLES

In colloidal systems, whether sol or gel, as in most liquids, there is little question but that groups, minute aggregates, of molecules exist as individuals. To such aggregates Nägeli long ago gave the name "micelle." Their existence has been accepted as a fact not only in fluids, but, by most biologists, in organized bodies as well. Of course, much depends upon the definition of the word micelle, but when accepted as designating an entity, there may be a question as to whether such individuals exist as units in the more permanent structures which have been built up by vital processes. Proof of their existence in organized structures has been offered from many different fields of investigation including that of X-rays. It is only the latter in which we are interested here. Earlier in this paper in connection with X-ray reflection from cellulose fibers, it may be recalled that small blocks (Fig. 4) were assumed, for convenience of explanation, to exist as minute crystalline

components of the wall. Investigators have accepted their existence and, by measuring the width of the X-ray diffraction lines, have computed their dimensions (14). It must be remembered that in order to produce reflection, the molecular layers must be very uniform in spacing and in parallelism. A deviation of a very small part of a degree will cause the reflection from one plane to annul that from another in the same block. Thus if a minute piece of the cell wall, say as large as two of the small blocks mentioned, were bent very slightly in the middle, then one-half of it could be in a reflecting position while at the same time the other half would not, and, so far as X-ray reflection is concerned, the block would be only as large as the part which was in a reflecting position. A piece of material which was bent and warped in many places, only very slightly away from a uniform flatness, would give the effect of being made up of blocks set together unevenly. Any one who is accustomed to use the microscope much in biological work knows that a surface under high power may appear very irregular, which under low power was excessively smooth.

It seems then that the very minute warped and bent regions in organized structures might readily be mistaken for individual blocks, and measured by X-ray methods for micelles. Evidence from other sources leads one to believe that biological structures, even such as ramie fibers which show a considerable degree of uniformity in molecular arrangement, are not uniform throughout. In most cases they are layered structures with the interfaces between the layers lacking in orderly arrangement of the molecules. The layers, themselves, may be submicroscopic in thickness and are probably composed of still thinner layers. Their width and length are open to question, as also is the extent to which they may be connected tangentially, and perhaps radially, by anastomosing branches. Such a mesh-work structure seems to be not at all improbable, and if it does exist, the conception of the individuality of the micelle in such structures must be abandoned. When put into a colloidal liquid system the material of these mesh-work structures must be thought of as having been torn into minute particles which may then be considered as micelles. In many cases these micelles may have a regularity in the arrangement of their molecules, which approaches that of simple crystals.

FORCES INVOLVED

It may not be out of place, in concluding, to mention some of the concepts which emerge from studies of molecular structure such as have been reviewed briefly in this article. Obviously there are certain forces involved in holding atom to atom and molecule to molecule. An adequate discussion of these forces lies beyond the scope of this paper, but at least a word concerning them seems necessary. In a very general way it may be said, that primary valence forces hold the atoms together into a molecule, and further, that they are very strong forces; while on the other hand, the forces which hold molecules together are relatively much weaker. The latter may be spoken of collectively as van der Waals' forces. Primary valence forces are usually thought of as chemical forces, since in order to separate atom from atom a chemical reaction is necessary. In a cellulose chain the glucose residues are held together by primary valence forces acting through an oxygen bridge. In order to separate the residues from one another a chemical re-

action, hydrolysis, is necessary; but to separate the chains laterally, a simple swelling process is all that is needed to overcome the van der Waals' forces.

With these two conceptions in mind, one may visualize a possible process of cell wall growth (19). By diffusion, glucose molecules approach the surface of a cell wall. They are oriented into the proper positions necessary for units of the cellulose lattice and held here by van der Waals' forces. Their positions bring two OH groups of two adjacent glucose molecules close together, resulting, if conditions are suitable, in a chemical reaction in which one molecule of water is split off, and in the formation of the oxygen bridge between the glucose residues. A continuation of this process produces long chains of glucose residues having a strength due to the primary valence forces involved in the formation of the oxygen bridge. Such a structure should have great strength for small weight, for it is a very open structure, relatively, in terms of atomic structure.

At the surface of the wall one may conceive a layer one chain thick and many chains in width, literally a unimolecular sheet, with the chains held together laterally by van der Waals' forces. Since the glucose units of the chains are uniformly spaced they present a surface, with some sort of mosaic design, towards the protoplasmic matrix which forms an interface with it. The probability of a mosaic pattern being formed in the protoplasmic materials immediately adjacent is, to say the least of it, intriguing (33).

When one considers this surface layer in connection with a similar layer underneath it and visualizes more layers still deeper in the wall, as constituting the thickness of the cell wall, a molecular picture of a membrane begins to take form. But we are going beyond the limits set for this paper.

To one who is not conversant with this field of investigation, and who has managed to endure to this point, it is hoped that the spatial concept of the molecule may have a somewhat clearer meaning than heretofore; and that the concept may prove useful when thinking of activities which occur in the protoplasmic matrix of organisms, and of structures which are produced through so-called vital processes.

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THE EVOLUTION OF THE RESPIRATORY FUNCTION OF THE BLOOD

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(Contribution No. 13, Woods Hole Oceanographic Institution)

According to current doctrines the mammals are the product of an evolutionary development which is traced back through the lower classes of vertebrates and is usually considered to have had its origin among the invertebrate phyla. In recent years the respiratory function of mammalian blood has been studied in great detail. Considered as a physico-chemical system concerned with the transport of oxygen and carbon dioxide, its characteristics are now well known and in many ways satisfactorily understood (35). Recent publications make it possible to compare these properties of the blood in at least one or more representatives of the various classes of lower vertebrates and of certain invertebrates. One can consequently inquire what changes in the characteristics of the blood parallel the supposed evolutionary development.

In considering the evolution of the vertebrates certain general tendencies are apparent which have an obvious relation to the respiratory function of the blood. In the first place, the change from an aquatic to a terrestrial habit of life involves a profound alteration in the method of aerating the blood and in the conditions to which the blood is exposed in the respiratory organs. In the second place, the general tendency throughout the development has led to organisms increasingly capable of intense activity. This has required the development of more effective arrangements for the circulation of the blood and the transport of gases by it in order to care for greater metabolic requirements. One of the factors which has favored the greater activity of which the birds and mammals are capable is the development of a constant, high body temperature which has at the same time fixed rather definitely one of the conditions under which the respiratory function of the blood takes place.

The transport of oxygen by vertebrate blood is due practically entirely to the hemoglobin present in it. Consequently the conditions under which oxygen is carried depend upon the specific properties of this substance. The transport of carbon dioxide, on the other hand, while depending in large part on reactions in which hemoglobin is involved, is a less specific phenomenon, since other proteins such as serum albumen and globulin and certain inorganic substances play a considerable rôle. The transport of carbon dioxide is consequently dependent in its details upon the general processes whereby the kidney and other organs regulate the composition of the blood.

The hemoglobins are substances which may be decomposed into hematin and a protein, globin. The former compound contains iron in complex combination with protoporphyrin. It is to the hematin fraction that the transport of oxygen by hemoglobin is due, oxygen being combined with hemoglobin in strict

proportion to its iron content. The hematins derived from the hemoglobin of different species appear to be identical, since it has been shown that the same porphyrin may be derived from the hematin of mammals, fish, and the insect, *Chironomus* (29) (48).

In addition to hemoglobin there are three other well-defined respiratory proteins. Chlorocruorin, which is most nearly related to hemoglobin, is found in the blood of certain worms,—the Sabellidae, Serpulidae, and Chlorhaemidae. Chlorocruorin is also a protein-hematin compound. The hematin, however, is not the same substance as that found in hemoglobin, being composed of a porphyrin distinct from that occurring universally in hemoglobin (32) (78) (79). Chlorocruorin has never been found in blood corpuscles, but occurs in solution in the blood and body fluids.

Hemerythrin is another respiratory protein containing iron which occurs in certain worms. This pigment does not appear to contain a hematin or a porphyrin and in certain other respects shares the characteristics of the hemocyanins (15) (53). Hemerythrin occurs in blood corpuscles, never in solution in the plasma. It is found in the blood of the Sipunculoidea, and in the polychaet, *Magelona*.

The hemocyanins, which are copper-protein compounds, show no chemical relation to hemoglobin and take no part in the respiratory function of the bloods which may be considered a part of the evolutionary series with which we are concerned.

The distribution of the hemoglobins in the animal kingdom is wide and, when considered from the point of view of evolutionary doctrine, puzzling. Hemoglobin is the universal respiratory pigment of the blood of vertebrates, being the only substance serving this function in the phylum and occurring in all its members with the exception of *Amphioxus*. It is also the dominant respiratory pigment in the annelid worms, occurring in the majority of polychaets and echiuroids, in many oligochaets and in some leeches (16) (50) (51) (64). In addition to these groups, where its distribution is somewhat general, hemoglobin is found in a variety of isolated instances in other parts of the animal kingdom, as the summary in Table 1 indicates.

In addition to its occurrence in the blood, hemoglobin is found in other tissues, particularly the muscles and nervous tissues of many animals. In the former situation it occurs in some forms which do not contain hemoglobin in their blood, for example, in the pharyngeal muscles of certain gastropods whose blood contains hemocyanin as the respiratory pigment (50) (54).

The occurrence of hemoglobin in these random cases among natural groups whose other members as a whole do not possess this substance is surprising from the evolutionary point of view. One can only conclude that it has been possible for hemoglobin to arise more or less independently in a variety of different groups. The difficulty is somewhat relieved by the discovery that protophorphyrin, the principal specific building-stone of hemoglobin, is widely distributed throughout the animal kingdom and by the demonstration that cytochrome, which like hemoglobin appears to be a porphyrin derivative, and allied pigments are very general in their distribution among plants and animals (1) (28) (30) (46). These considerations make it extremely dangerous to relate the vertebrate blood to that of any invertebrate group, for it appears quite possible that hemoglobin may have arisen *de novo* in the blood of the ancestral vertebrates just as it appears to have in

Chironomus, *Planorbis*, and other isolated instances. On the other hand, if the distribution of hemoglobin in the animal kingdom has any relation to evolutionary tempting to compare conditions existing in the blood of the vertebrates with those of lower animals, we are forced to assume this point of view, since the worms are

TABLE 1

Distribution of Hemoglobin in the Blood of Animals

PHYLUM	CLASS	GENUS
Platyhelminthes	Turbellaria	*Derostoma* (56) *Syndesmis* (58)
	Nemertinea	*Drepanophorus* (39) *Polia* (50)
Nemathelminthes	Nematoda	*Ascaris* (46)
Molluscoidea	Phoronida	*Phoronis* (50) *Phoronopsis* (60)
Echinodermata	Holothuroidea	*Thyone* (16) *Cucumaria* (16) (71) *Caudina* (48a) *Malpadia* (48a)
Annulata	Polychaeta	Many cases (16) (64)
	Oligochaeta	Many cases (16) (64)
	Echiuroidea	*Thalassema* (51) *Urechis* (61)
	Hirudinea	Some cases (16)
Arthropoda	Crustacea	*Daphnia* (50) *Cheirocephalus* (50)
	Insecta	*Chironomus* (50)
Mollusca	Pelecypoda	*Solen* (50) *Arca* (16) (66) *Cardita* (85) *Pectunculus* (16)
	Gastropoda	*Planorbis* (50)
Chordata	All vertebrates	(50)

history, then emphasis must be placed on the fact that the annelids are the only invertebrate group in which the occurrence of hemoglobin is really general. In attempting to compare conditions existing in the blood of the vertebrates with those of lower animals, we are forced to assume this point of view, since the worms are the only group affording pertinent data with which we may deal.

The conditions existing in the blood of the polychaet worms have been reviewed

amply by Romieu (64), who points out the great diversity of conditions occurring within this group. With a little freedom, his classification may be made to serve for the entire series in which hemoglobin occurs. Leaving out of account the large number of animals in which respiratory proteins do not occur, we find among the invertebrates two general situations which appear to include most cases. In those animals in which there exists a definite circulatory apparatus the respiratory pigment usually occurs in solution in the blood, which is sharply separated from a coelomic fluid, rich in leucocytes, and free from respiratory proteins. This is the most common situation among the polychaet worms and in the oligochaets. It is also the condition obtaining in those worms in which chlorocruorin occurs, except that in some at least of these forms chlorocruorin occurs also dissolved in the coelomic fluid, as in *Spirographis* and *Siphonostoma*.

In contrast there is a considerable number of animals in which the respiratory protein is enclosed in corpuscles and this situation occurs principally in those forms in which the vascular system is degenerate or lacking, the corpuscles being suspended in the coelomic fluid. This is the condition occurring in *Glycera*, *Capitella*, and *Polycirrus haematodes* among the polychaets, in the echiuroid *Urechis*, and in the sipunculoids *Phascolosoma* and *Sipunculus* in which the erythrocytes contain hemerythrin.

Two species of polychaets, *Terebella lapidaria*, and *Travisia Forbesii*, combine the two foregoing conditions. In these worms the vascular blood contains hemoglobin in solution, whereas the coelomic fluid is provided with abundant erythrocytes.

Finally, a single species of worm, *Magelona papillicornis*, exhibits a condition strictly comparable to that found in the vertebrates, that is, a blood confined to definite vessels in which the respiratory pigment is carried in blood corpuscles. The resemblance to the vertebrate condition is furthered by the fact that in *Magelona* alone, among all invertebrates, the blood corpuscles appear to be anucleated. The comparison to the vertebrate condition breaks down entirely, however, when it is considered that in *Magelona* the respiratory protein is hemerythrin.

The condition observed in *Phoronis*, *Phoronopsis*, and certain Nemertinea may best be classed with *Magelona*, for in these forms the blood is confined to definite vessels and contains erythrocytes bearing hemoglobin. The vascular system of the Phoronidae, however, is organized on somewhat different lines from those followed in the case of the worms and vertebrates.

From the foregoing it appears that although the situation under which hemoglobin occurs in the body fluids of the invertebrates is most varied, conditions which are strictly comparable to those found in the vertebrate series are rare and occur in rather isolated cases.

The general character of the erythrocytes found among the vertebrates is well known. It will suffice to recall that in all mammals, except in the camels, they are circular disc-shaped bodies. In the camels they are flattened ellipsoids. In the mammals they contain no nuclear material; in all other vertebrates they possess well-marked nuclei. In the birds, reptiles, amphibians and in all fishes except the cyclostomes, the erythrocytes are flattened ellipsoids; in the cyclostomes the shape is discoid (57).

The erythrocytes of the invertebrates are nucleated bodies, spherical in *Thalassema* (51) and *Urechis* (61), or flattened

discs of nearly circular outline, in *Terebella lapidaria*, *Glycera* (64), *Phascolosoma*, *Arca*, and *Thyone* (16a). The corpuscle is surrounded by a definite membrane which appears to enclose a distinctly fluid cytoplasm. In addition to the dissolved hemoglobin, the cytoplasm frequently contains highly refractive bodies, which Romieu considers to be fatty in nature, and also colored granules. These are thought to be accumulated waste materials by Romieu, who identifies them as a uratic pigment. Similar bodies are frequently very numerous in the erythrocyte of *Urechis*. Baumberger and Michaelis (8) consider the pigment to be hematin in this form and present evidence that the accumulation of hematin is utilized in forming the pigments of the egg. Romieu also presents a similar view with regard to the utilization of the pigments of the erythrocytes of *Terebella*. Rather extensive patterns of reticulation, resembling those of vertebrate erythrocytes, appear in the corpuscles of *Glycera*, *Phascolosoma*, *Arca*, and *Thyone* on treatment with brilliant cresyl blue (16a).

The invertebrate erythrocyte appears in general to be less highly differentiated than the vertebrate red blood corpuscle. Romieu's investigations indicate that the red cell found in the coelomic fluid of worms is strictly homologous to the vertebrate erythrocyte, the young corpuscle passing through all the phases which are known among the vertebrates. Jordan (40) believes that if one assumes a continuous evolution from invertebrates to vertebrates, a transition can be traced from segmented worms to cyclostome fishes in which the lymphogenous organ of invertebrates may be regarded as a very primitive spleen.

The apparent relation between the erythrocyte of the vertebrate blood and the corpuscle of the coelomic fluid in the invertebrates deserves some emphasis. Physiologists have tended to consider the occurrence of hemoglobin in solution in the blood of worms as representing a primitive condition and as such the evolutionary forerunner of blood containing erythrocytes. This view is definitely taken by Romieu (64), who suggests that the development of the coelomic erythrocyte has rendered the vascular system useless and has led to its degeneration in many forms. It has been maintained that the raison d'être of the erythrocyte is to permit hemoglobin to exist in the blood in quantities greater than would be possible were it dissolved directly in the circulating fluid (3). While it cannot be denied that the blood of the higher vertebrates contains more hemoglobin than could be dissolved in a fluid adapted to circulate in the vascular system, this possibility does not appear to have been realized in the invertebrate stage of evolution, for *Arenicola* and *Spirographis*, which carry their respiratory pigments in solution, have blood with a greater oxygen capacity than *Urechis* and the other invertebrate forms in which oxygen is transported in corpuscles (61). When these considerations are taken in connection with the fact that red blood corpuscles exist in such primitive forms as the nemerteans and *Phoronis*, one may properly question whether the occurrence of hemoglobin in solution in the blood of worms does not represent a rather specialized development. It seems significant in this connection that when hemoglobin occurs in solution it is always confined to a closed vascular system. It is now understood that the proteins of the plasma of the blood of the higher vertebrates play an important rôle in the hydrostatic equilibrium which determines the exchange of water through the capillary wall. It is known that fluids

free from protein or other substances of large molecular size cannot be retained within the vascular system. Is it not probable that the hemoglobin dissolved in the blood of the worms serves a function in counterbalancing the effect of the pressure developed within the blood vessels analogous to that exerted by the plasma proteins of the vertebrates? This action would not occur if the hemoglobin were retained in corpuscles unless other specialized serum proteins were developed to serve the purpose.

These considerations suggest that the hemoglobin which exists in solution in the blood of the invertebrates supplies a factor necessary in the hydrostatic equilibrium on which the existence of vascular blood depends. In the vertebrates the general occurrence of plasma proteins fulfills this requirement and makes it possible for hemoglobin to be confined to corpuscles suspended in the vascular fluid.

Certain quantitative facts appear to support this view. First, there is evidence of an increase in the concentration of plasma proteins in the evolutionary series. The body fluids of invertebrates are in general extremely poor in protein except for those cases where hemocyanin and the other respiratory proteins occur in solution. Among the worms, for example, there are no proteins in the coelomic fluid of *Echiurus pallasii* (68). In *Sipunculus* the concentration of protein in the coelomic fluid is 0.11 per cent (17); in *Urechis* 0.11 per cent (45). Among the vertebrates a progressive increase in the concentration of plasma protein occurs, the following values being recorded; skate, 2.4–3.1 per cent (20); dogfish, 2.2–4.4 per cent; goosefish, 1.4–2.2 per cent; menhaden, 0.72–2.9 per cent; bullhead, 3.9–4.8 per cent (52a); lungfish, 5.5 per cent (69); frog, 1.5–4.29 per cent (13); crocodile, 3.69 per cent (19); alligator, 4.4–5.8 per cent (2); snapping turtle, 4.8 per cent (35); dog, 6.1–6.7 per cent (21); man, 6.5 per cent (35). The increasing values appear to parallel the development of a cardiovascular system capable of containing blood at increasing pressures. In the second place, when hemoglobin occurs in solution in the blood, its concentration is comparable to that of the serum proteins in the lower vertebrates. It is estimated that the blood of *Planorbis* contains 1.5 per cent hemoglobin, that of *Arenicola* 3.25, that of *Lumbricus* 3.7 per cent (41). It is also pertinent that in the blood of *Syllidiens*, which contains no hemoglobin, the vascular blood contains a much larger quantity of protein than the perivisceral lymph (64). A more extensive investigation of the plasma proteins in the invertebrates and lower vertebrates is very desirable from this point of view.

THE QUANTITY OF HEMOGLOBIN IN THE BLOOD AND IN THE ERYTHROCYTE

Practical indication of the quantity of hemoglobin contained in the blood of various animals is given by measurements of the amount of oxygen with which it will combine when in equilibrium with atmospheric air. Representative data for various animals are presented in Table 2. In general there is an increase in the oxygen capacity of the blood in the course of the evolutionary series, the highest values of about twenty volumes per cent being found in the birds and mammals, the lowest values among the invertebrates. Within each group there is considerable variation which may be related directly to the activity of the various species. This is particularly well shown among the fishes (33). Table 2 also shows the way in which the volume of the blood occupied by cells tends to increase in the course of the evolutionary series. The ratio of

The Oxygen Capacity and Cell Volume of the Blood of Various Animals

SPECIES	OXYGEN CAPACITY OF BLOOD	CELL VOLUME	OXYGEN CAPACITY OF 100 CC. CELLS
	vol. per cent	*per cent*	*vol. per cent*
Mollusks:			
Cardita sulcata (85)	1–2		
Pectunculus violaceus (85)	1–2		
Arca inflata (66)		6 5	
Planorbis corneus (10) (52)	1.0–2.5	None	
Insects:			
Chironomus (52)	6	None	
Worms:			
Urechis caupo (61)	2.7–7.2	18–40	9 3–17
Glycera siphonostoma (85)	2.6–3 0		
Arenicola marina (10)	8.4–9.7	None	
Spirographis Spallanzanii (32)	8.1–10*	None	
Fishes:			
Skate, *Raia ocellata* (20)	4.2–6.0	20	30
Dogfish, *Mustelus canis* (25)	5.5–7.8		
Goosefish, *Lophius piscatorius* (65)	5.1	15.5	33
Toadfish, *Opsanus tau* (65)	6.2	19.5	32
Puffer, *Spheroides maculatus* (65)	6.8	17.5	39
Scup, *Stenotomus chrysops* (65)	7.3	32.6	23
Sea robin, *Prionotus carolinus* (65)	7.7	24	32
Carp, *Cyprinus carpio* (23) (80)	11.5–16 8	40	35
Mackerel, *Scomber scombrus* (65)	15.8	37	43
Eel, *Anguilla japonica* (43)	10 2–15.6	31–41	35
Amphibians:			
Amphiuma tridactyla (67)	2.5–8.4	14–28	25
Rana esculenta (23) (84)	13.5–23	41	33
Reptiles:			
Snapping turtle, *Chelydra serpentina* (35)	5.9	20.4	29
Tortoise, *Pseudemys concinna* (70)	6.6–11	9.8–22	50
Alligator (38)	12	14 5	83
Crocodile, *Crocodilus acutus* (19)	8–10	18–24	43
Birds:			
Sparrow (23)	14.5	37	39
Serin (23)	14	36	39
Pigeon (23)	21	53	40
Surf scooter (60)	22	45	47
Crow (23) (83)	17–22	54	40
Owl, *Syrnium aluco* (83)	19		
Mammals:			
Man (24)	21	46	46
Horse (24)	16.7	36	47
Sheep (24)	15.8	39	41
Rat (24)	18.7	47	40
Sea lion, *Eumetopias stelleri* (31)	19.8	29	68
Porpoise (70a)	42–45		
Porpoise, *Phocaena phocaena* (32b)	22.2	35	63

* Blood contains chlorocruorin.

oxygen capacity to the volume of cells in a unit quantity of blood, tabulated in the fourth column, shows how the concentration of hemoglobin varies in the red corpuscles of the different groups. These data exhibit a very definite trend. The concentration of hemoglobin in the erythrocyte of *Urechis* is much less than that observed in any vertebrate. The values are relatively constant among the fish and amphibians and are highest in certain reptiles, birds, and mammals. The highest values are found in the aquatic mammals. (The exceptionally high value obtained for the alligator would appear to require confirmation in view of its dissimilarity from that characterizing the crocodile and other cold-blooded vertebrates.) The progressive morphological differentiation which the erythrocytes show throughout the animal series is accompanied by a definite increase in the concentration of hemoglobin within them.

THE EQUILIBRIUM BETWEEN HEMOGLOBIN AND OXYGEN

The equilibrium between oxygen and the hemoglobin of the blood is commonly expressed by the so-called "oxygen dissociation curve" in which the amount of oxygen combined with the blood, expressed as a fraction of the total oxygen capacity, is plotted against the partial pressure of oxygen with which the blood is in equilibrium (Figs. 1 and 2). Although more than half a dozen theories have been proposed, the interpretation of the exact shape of such curves is not altogether clear (5) (27). For purposes of description the oxygen dissociation

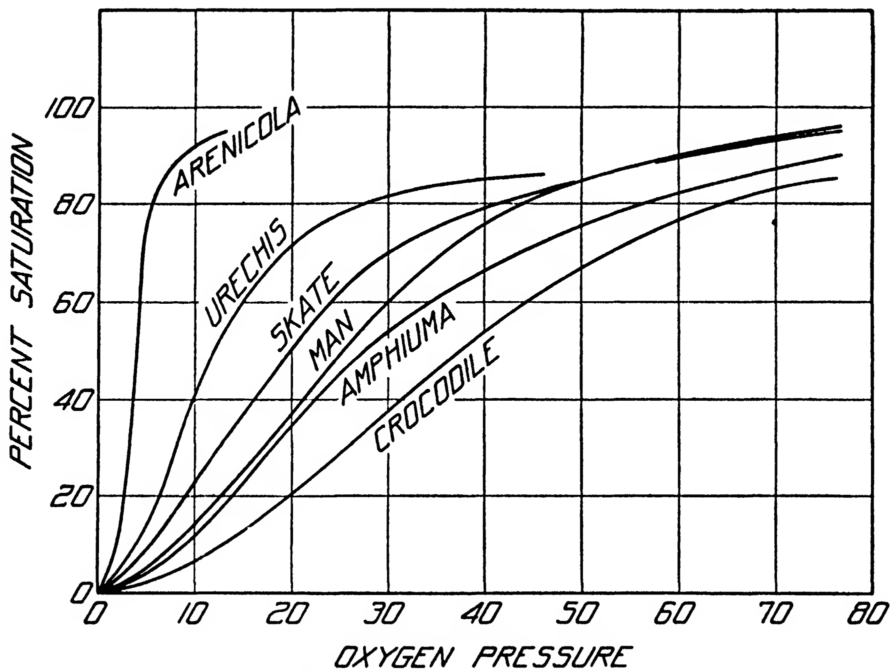

FIG. 1. OXYGEN DISSOCIATION CURVES OF TYPICAL SIGMOID SHAPE

Ordinate, percentage of saturation with oxygen; abscissa, oxygen pressure in mm. Hg. *Arenicola* (6), 20°C., pH 6.9; *Urechis* (61), 19°C., pH 7.1; skate (20), 10.4°C., pH 7.8; man (35), 38°C., pH 7.47; *Amphiuma* (67), 26°C., carbon dioxide pressure 43 mm.; crocodile (19), 29°C., pH 7.2.

curves of most bloods are defined with sufficient precision by Hill's (37) equation

$$y = \frac{Kx^n}{1 + Kx^n}$$

in which y is the percentage of the hemoglobin oxygenated at the partial pressure of oxygen, x. The general shape of the oxygen dissociation curve is related to the value of n. For a hyperbolic curve, n is 1.0; at higher values of n (above about 1.4) the curve acquires a double inflexion or S-shape which becomes more marked as the value of n increases.

The shape of the oxygen dissociation curve, as indicated by n, appears to be affected little or not at all by temperature (11) (81) and by changes in hydrogen ion concentration or carbon dioxide pressure (5) (27). This fact simplifies the comparison of the shape of the oxygen dissociation curves of different species, since the differences in the conditions under which the measurements have been carried out may be neglected. The value of n characteristic of different bloods varies considerably as the following table shows:

	n
Skate (20)	2.0
Eel (44)	1.0
Carp (80)	1.3
Amphiuma (67)	1.8
Turtle (70)	1.5
Man (5)	2.2
Pig (11)	2.0–2.6
Ox (11)	2.3–3.0

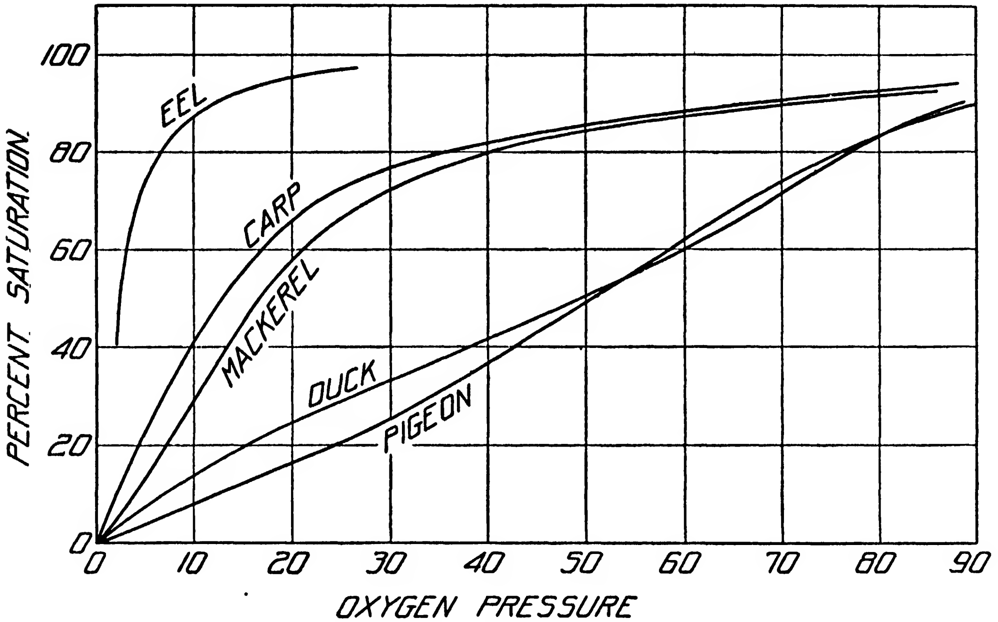

FIG. 2. OXYGEN DISSOCIATION CURVES OF ATYPICAL SHAPE

Ordinate, percentage of saturation with oxygen; abscissa, oxygen pressure in mm. Hg. Eel (44), 17°C., carbon dioxide pressure not given; carp (80), 18°C., carbon dioxide pressure 30 mm.; mackerel (65), 20°C., carbon dioxide pressure 1 mm. Hg.; duck (81), 42°C., carbon dioxide pressure 40 mm.; pigeon (81), 42°C., carbon dioxide pressure 40 mm.

The bloods of the great majority of animals show a distinctly S-shaped oxygen dissociation curve, as indicated by the higher values of n. This is true of the mammals, the crocodile (19), *Amphiuma*, the skate, and the worms *Urechis* (61)

and *Arenicola* (6). The oxygen dissociation curves of the blood of fish appear to be somewhat exceptional in that the sigmoid character of the curve is less pronounced (in the mackerel) or is lacking as in the sea robin, toadfish (65), and carp (80). The blood of the eel is said to have a purely hyperbolic oxygen dissociation curve, but the evidence for this cannot be considered convincing. Figure 2 illustrates the form of some of these atypical oxygen dissociation curves.

Studies of the oxygen dissociation curves of fishes made since the foregoing was written display a number of unique conditions not previously described and throw some light on the nature of the atypical oxygen dissociation curves (32c).

The oxygen dissociation curve of the birds is also exceptional, and cannot be described by Hill's equation (81) (82). That of the duck has the curious shape shown in Fig. 2. Those of the pigeon and goose are intermediate in form between that of the duck and the more typical sigmoid curve observed in most vertebrates. Such curves have not been described for other bloods containing hemoglobin. They are, however, characteristic of the bloods of the horse-shoe crab, *Limulus*, and the gastropod, *Busycon*, which contain hemocyanin (60).

The comparative study of the equilibrium of blood with oxygen is complicated by the variety of factors which influence the degree of oxygenation which will be attained under any given oxygen pressure. This relation is defined by the value of the oxygen dissociation constant K in Hill's equation. Certain of these factors are inherent in the chemical properties of the medium in which hemoglobin exists in the blood. Others, such as temperature, are determined purely by the environmental conditions in most forms, while some factors, such as carbon dioxide tension and hydrogen ion concentration, are influenced alike by physiological and environmental considerations. It is frequently difficult to compare the data obtained by various observers because each has been concerned with a somewhat different aspect of the problem and it is infrequent that data are obtained under strictly comparable conditions. It is consequently desirable to consider some of the factors affecting the equilibrium of oxygen with hemoglobin with a view to discovering to what extent these difficulties may be overcome.

The effect of temperature upon chemical equilibria is expressed by an equation derived from the van't Hoff isochor:

$$\frac{K_2}{K_1} = e^{-q\,(T_2 - T_1)/RT_1T_2}$$

in which K_1 and K_2 are the equilibrium constants for the reaction at absolute temperatures T_1 and T_2 and q expresses the heat evolved when one gram molecule of the reaction product is formed. This equation appears to supply a satisfactory basis with which to deal with variations in the equilibrium of hemoglobin and oxygen under the influence of temperature.

The value of q includes not only the heat evolved when hemoglobin combines with oxygen, but, as commonly measured, the heat of solution of oxygen and such other heat exchanges as accompany the altered equilibria which occur when blood is oxygenated. The latter are due chiefly to the fact that hemoglobin becomes a stronger acid when oxygenated and in consequence a new equilibrium is established in the distribution of base between hemoglobin, bicarbonate and perhaps other weak acids. Since it has been shown that in the case of the blood of the pig, ox (11), pigeon, duck, and goose (81) (82) the shape of the oxygen dissociation curve is unchanged by variations in temperature, in practice the reciprocal of p_{50},

the oxygen tension at which the blood is half saturated with oxygen, may be substituted for the equilibrium constant. The data may be expressed by plotting the logarithm of p_{50} against the reciprocal of the absolute temperature when it is found that the experimental points fall on a line which is straight, or nearly so, and with a slope which is determined by q. When blood is studied under suitable conditions, q has very nearly the same value in a considerable number of species. This is brought out by the fact that the various curves illustrated in Fig. 3 have about the same slope. Such similarity is only to be expected if the heat of reaction between hemoglobin and oxygen is about the same in all species and provided the conditions are such that the accessory reactions accompanying oxygenation absorb an equal fraction of the heat of reaction in each case. These facts point to a general similarity in the blood of different forms in respect to the thermodynamic changes involved in the combination of hemoglobin with oxygen. When the experiments are carried out at diminishing carbon dioxide pressures (7) (81), in the absence of carbon dioxide (11), or at constant hydrogen ion concentration (26), temperature changes have a larger effect upon the value of the equilibrium constant, and the heat of reaction is larger when measured directly, than is the case in experiments done under constant carbon dioxide pressures of normal physiological value. This is explained by the diminished degree to which heat is absorbed

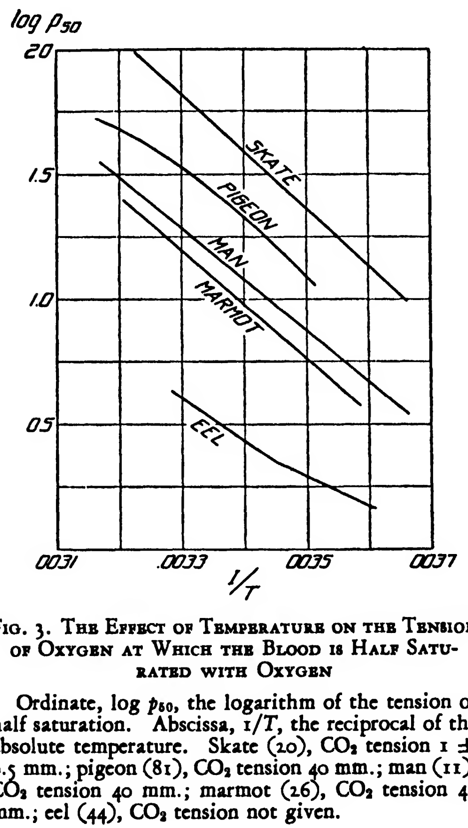

FIG. 3. THE EFFECT OF TEMPERATURE ON THE TENSION OF OXYGEN AT WHICH THE BLOOD IS HALF SATURATED WITH OXYGEN

Ordinate, log p_{50}, the logarithm of the tension of half saturation. Abscissa, $1/T$, the reciprocal of the absolute temperature. Skate (20), CO_2 tension 1 ± 0.5 mm.; pigeon (81), CO_2 tension 40 mm.; man (11), CO_2 tension 40 mm.; marmot (26), CO_2 tension 40 mm.; eel (44), CO_2 tension not given.

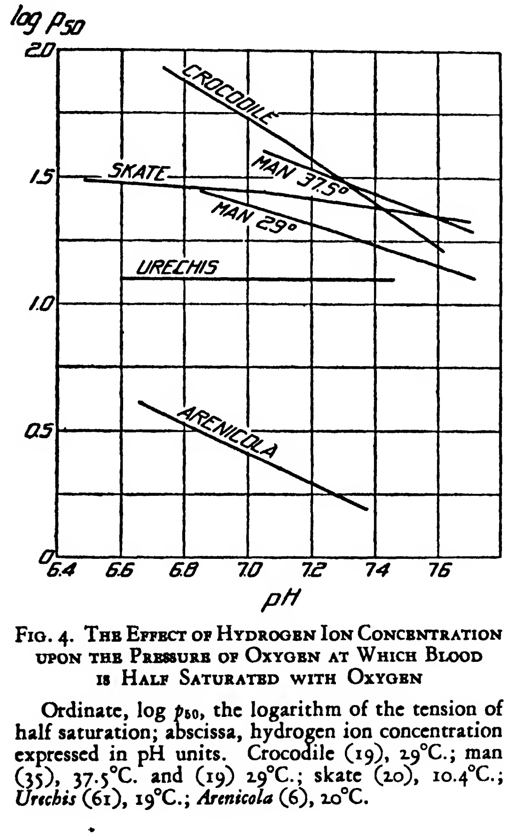

FIG. 4. THE EFFECT OF HYDROGEN ION CONCENTRATION UPON THE PRESSURE OF OXYGEN AT WHICH BLOOD IS HALF SATURATED WITH OXYGEN

Ordinate, log p_{50}, the logarithm of the tension of half saturation; abscissa, hydrogen ion concentration expressed in pH units. Crocodile (19), 29°C.; man (35), 37.5°C. and (19) 29°C.; skate (20), 10.4°C.; *Urechis* (61), 19°C.; *Arenicola* (6), 20°C.

through changes in the quantity of base combined with the hemoglobin.

The effect of hydrogen ion concentration upon the equilibrium of various bloods with oxygen is more difficult to deal with. The hydrogen ion concentration, depending as it does on the ratio of acids and bases in the blood and upon the equilibria which determine the distribution of electrolytes between corpuscles and plasma, is defined by a multiplicity of factors. One may arrive at an approximation to the hydrogen ion concentration if one knows the pressure of carbon dioxide in the system and the amount of carbon dioxide bound as bicarbonate. Unfortunately, not many studies of the blood of the lower animals provide these data simultaneously, attention usually being limited to the effect of carbon dioxide pressures upon the oxygen dissociation curve without reference to the bicarbonate content. However, a limited amount of data is available which enables one to compare the effect of hydrogen ion concentration upon the equilibrium of different kinds of blood with oxygen. These data are summarized in Fig. 4, in which the logarithm of the oxygen tension at which the hemoglobin is half saturated with oxygen is plotted against the pH of the blood. The facts summarized in this figure make it clear that the various bloods vary distinctly in regard to the effect of hydrogen ion concentration upon the equilibrium of blood with oxygen. In some bloods, as that of the skate at acid reactions, and that of *Urechis*, the hydrogen ion concentration has little or no effect on the oxygen equilibrium. In most of the bloods which have been studied the effect is marked, its magnitude differing from species to species. If the data presented in Fig. 4 are corrected to some uniform temperature employing the principle set forth above, the agreement among the various species is not improved. It seems probable that these variations are due to specific differences in the hemoglobin of the different animals. From the available data it is impossible to see any definite tendencies which may be related to the systematic classification of the animals.

A somewhat special relationship between hydrogen ion concentration and the combination of hemoglobin with oxygen appears in the blood of certain teleost fishes. From studies upon the blood of the mackerel, sea robin, and toadfish, Root (65) has concluded that increasing concentrations of carbon dioxide not only influence the oxygen dissociation constants of the blood but bring about a decided decrease in the oxygen capacity of the hemoglobin. It appears as though certain of the prosthetic groups concerned in binding oxygen to the hemoglobin molecule were inactivated. The effect is also produced by lactic acid so that it cannot be attributed specifically to carbon dioxide. Similar phenomena do not appear to have been recorded for the bloods of other groups.

It is apparent that the bloods of various animals differ markedly in the conditions governing the equilibrium with oxygen. This fact may be most simply explained on the assumption that the hemoglobins of the different species are chemically distinct. For this view there is some evidence of a spectroscopic, crystallographic and chemical sort (5) (34) (48a) while immunological experiments indicate that the carbon monoxide hemoglobin from different mammals is species specific (9).

The nature of the chemical differences in different hemoglobins is, however, still quite illusory. Since the porphyrin portion of all hemoglobins appears to be the same (29) (48), it has generally been

suspected that the specific qualities of hemoglobin depend upon the globin fraction of the molecule. Investigations of globin as yet do not appear to have demonstrated the nature of such specific differences if they exist (63).

It has also been suggested that the specific differences may be due to the occurrence of hemoglobin within semi-permeable corpuscles which enables a characteristic chemical environment to be secured for the hemoglobin of each species and thus determines its specific properties in each organism. Against this view it may be pointed out that the properties of the blood of the dog are very similar to those of the blood of man in spite of the great differences in the composition of the corpuscular electrolytes in these species (21). The two views are not mutually exclusive. In the absence of any studies of the properties of the purified proteins of the lower forms it is impossible to evaluate the importance of either possibility.

THE EQUILIBRIUM OF THE BLOOD WITH CARBON DIOXIDE

Carbon dioxide is transported in the blood as bicarbonate which results from the union of this gas—as carbonic acid—with base derived from hemoglobin, serum proteins and other buffers. It is not surprising consequently that the carbon dioxide dissociation curves of most animals are similar in form, and differ chiefly in the quantity of bicarbonate formed under a given carbon dioxide pressure. The curves shown in Fig. 5 illustrate this. It should be noted that the height of the curves from the base line follows in general the order of increasing hemoglobin content—as indicated by the recorded oxygen capacities of the blood.

The blood of a certain group of animals exhibits carbon dioxide dissociation curves which differ distinctly from the typical form. These are the bloods of the turtle (70), frog (84), *Amphiuma* (67), and carp (80). The carbon dioxide dissociation curves of these forms illustrated in Fig. 6. are all very much higher and flatter than those of the bloods exhibiting the more usual condition and indicate a greater ability to combine with carbon dioxide than would be expected from the hemoglobin content. It has been shown that this form of curve is due to the retention in the blood of an unusually large quantity of bicarbonate (67) (70) relative to the hemoglobin concentration. The effect is to be attributed to some peculiarity in the mechanism whereby the electrolyte content of the blood is regulated.

The buffering of the blood may be more precisely analyzed with the aid of the relation

$$\beta = \frac{-\Delta\ \mathrm{BHCO_3}}{\Delta\ \mathrm{pH}} = \frac{-\Delta\ \mathrm{BHCO_3}}{\Delta\ \log \dfrac{\mathrm{BHCO_3}}{\mathrm{H_2CO_3}}}$$

where the buffer value, β, is given by the ratio of the change in the bicarbonate content to the accompanying change in pH when the carbon dioxide pressure is increased (72). In the invertebrates it appears that the respiratory protein itself is the principal, if not the sole buffer substance. In *Limulus* the hemocyanin accounts for practically the total buffer effect (62). In *Urechis* the coelomic fluid appears to contain practically no buffers. The total buffer action is exerted by virtue of the corpuscles and their buffer value is equal to that of a quantity of human hemoglobin having an equivalent oxygen content (61). In the vertebrates also the buffer value of the blood as a whole when compared on the basis of equivalent oxygen capacity is approximately the same in the case of the skate (20), turtle (70), crocodile (19), dog (20), and man

(19). This general relation is reasonable, from the physiological standpoint, for under ordinary circumstances the carbon dioxide production of animals is nearly equal to oxygen consumption so that the needs for transport of the two gases go hand in hand. Table 3 summarizes the buffer value of the hemoglobin in the corpuscles of a number of different animals.

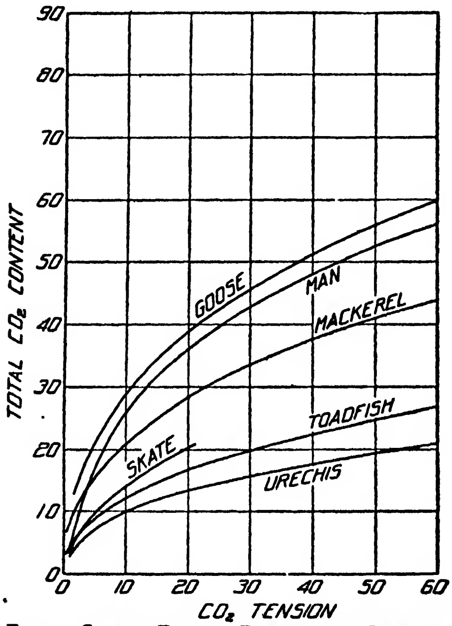

Fig. 5. Carbon Dioxide Dissociation Curves of Typical Shape

Ordinate, total carbon dioxide content measured in volumes per cent; abscissa, partial pressure of carbon dioxide measured in mm. Hg.

	Temperature °C	Oxygen capacity vol. per cent
Goose (83).........	40	20
Man (35)..........	38	20
Mackerel (65)......	20	15.8
Skate (20)..........	25	4.2–6.0
Toadfish (65)......	20	6.2
Urechis (61).........	18.5	3.9

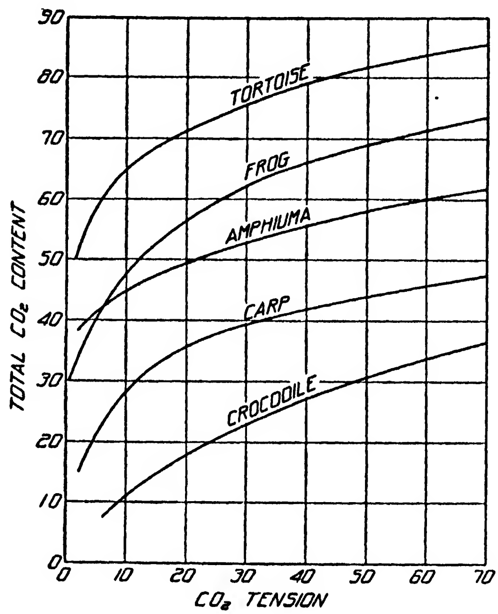

Fig. 6. Carbon Dioxide Dissociation Curves of Atypical Shape

Ordinate, total carbon dioxide content measured in volumes per cent; abscissa, partial pressure of carbon dioxide measured in mm. Hg.

	Temperature °C	Oxygen capacity vol. per cent
Tortoise (70)........	25	ca. 9
Frog (84)...........	15	ca. 10
Amphiuma (67)......	24	ca. 5
Carp (80)...........	15	ca. 9
Crocodile (19).......	29	9.25

The blood of vertebrates contains serum proteins which contribute definitely to the buffer value of the blood. It has been pointed out that the serum proteins are present in increasing concentration in the blood of the higher members of the vertebrate series. The relative part played by the serum proteins in buffering the blood against carbon dioxide is indicated in Table 4. The last column in this table indicates the relation of the buffer value of the serum proteins to their concentration in the blood and shows that the serum proteins in the skate and crocodile are more effective buffers than those in man. In this way they compensate in part for their lower concentration. Serum proteins are inferior buffers compared to hemoglobin as the recorded buffer values show.

In the Mammalia a large portion of the transport of carbon dioxide from the tissues to the lungs is effected as the result

TABLE 3

Buffer Values of Hemoglobin in Corpuscles at Physiological Reactions

SPECIES	BUFFER VALUE
	milliequivalents per gram hemoglobin
Urechis caupo, 19° (61)	0.169
Crocodilus acutus, 29° (19)	
Oxygenated	0.208
Reduced	0.143
Man, 29° (19)	
Oxygenated	0.183
Reduced	0.159
Man, 37.5° (18)	
Oxygenated	0.186
Reduced	0.166
Horse, 38° (74)	
Oxygenated	0.158
Reduced	0.147

In computing these values it is assumed that the equivalent weight of hemoglobin is 16,700 in all three species. The buffer value of the hemoglobin of the horse is based on studies of crystalline hemoglobin. That of other species is deduced from the study of whole blood.

this gas than will oxygenated blood. A similar effect has been observed in a large number of vertebrate bloods, although in some species it is necessary to concentrate the corpuscles before the effect is large enough to be clearly measurable. The effect is absent, or at least undetectable, in the blood of *Urechis* and of the skate. In these forms the reciprocal phenomenon, in which the presence of carbon dioxide affects the equilibrium between hemoglobin and oxygen, is absent (in *Urechis*) or very slightly developed (in the skate). Table 5 shows the magnitude of the change in bicarbonate content with change in oxygen content of the blood of a variety of animals. It is clear that this property of the blood varies definitely in different animals. Since the relation is a function of the properties of hemoglobin, it is probable that the differences observed in the various species are due to specific differences in their hemoglobins.

Although hemoglobin is the principal buffer substance concerned with the transport of carbon dioxide in the blood, this

TABLE 4

Buffer Values of Whole Blood, Separated Serum and Serum Proteins

SPECIES	TOTAL BLOOD OXYGENATED	TOTAL SERUM SEPARATED	SERUM PROTEINS
	milliequivalents per liter	*milliequivalents per liter*	*milliequivalents per gram protein*
Urechis caupo, 19° (61)	4.9	0	0
Skate, *Raia ocellata*, 25° (20)		4.63–6.48	0.193–0.209
Crocodile, *Crocodilus acutus*, 29° (19)	18.2	4.87	0.132
Dog, 37.5° (21)			0.093
Horse, 38° (75) (76) (77)	25.26		0.068–0.104
Man, 37.5° (36)	26.2	7.5	0.109

The buffer values for serum proteins of the horse are based on dialyzed serum (0.068) and purified serum proteins (0.104). The values for other animals are deduced from studies of plasma without correction for small amounts of other buffer substances.

of the fact that oxyhemoglobin is a stronger acid than reduced hemoglobin. At any carbon dioxide tension, reduced blood will combine somewhat more of gas, unlike oxygen, is not confined to the corpuscles, but is distributed according to well-recognized principles between the corpuscles and plasma (73). The hemo-

globin within the corpuscle is able to contribute to the buffer value of the plasma by reacting with anions, chiefly chloride, which migrate into the corpuscles from the plasma. The excess of cations thus set free in the plasma can consequently combine with carbonic acid to form bicarbonates. A similar phenomenon appears to occur in the blood of *Urechis* (61), the turtle (70), the crocodile (19), and the hen (14) and is doubtless a general phenomenon. In these forms the facts have not been studied in detail, and

TABLE 5

Effect of Oxygenation upon the Carbon Dioxide Content of Bloods at Constant Hydrogen Ion Concentration

The values are for a pH of 7.2 to 7.4 or when log $\frac{BHCO_3}{H_2CO_3} = 1.0$.

SPECIES	$-\frac{\Delta BHCO_3}{\Delta O_2}$
Urechis caupo (61)	0
Skate, *Raia ocellata* (20)	0
Toadfish, *Opsanus tau* (65)	0.45
Sea robin, *Prionotus carolinus* (65)	0.45
Mackerel, *Scomber scombrus* (65)	0.70
Amphiuma tridactyla (67)	0.54
Tortoise, *Pseudemys concinna* (70)	0.32
Snapping turtle, *Chelydra serpentina* (35)	0.22
Crocodile, *Crocodilus acutus* (19)	1.05
Caiman fuscus (19)	0.56
Goose (82)	0.50
Horse (75)	0.55
Man (35)	0.49

the quantitative aspects of the factors governing the distribution of anions and cations between corpuscles and plasma are not altogether clear. Since these animals all possess a relatively small volume of corpuscles, the phenomenon is of particular importance in that it allows most of the carbon dioxide to remain in the plasma where it is distributed through a volume large in comparison to that of the corpuscles which retain the hemoglobin.

RÉSUMÉ

The properties of the blood of the vertebrates and their forerunners display great variety in their quantitative relationships. In reviewing them, certain general tendencies have appeared. The variety of situations in which hemoglobin occurs in the invertebrates disappears in the vertebrates, among which the hemoglobin is universally confined within corpuscles in the blood. The morphological differentiation of the erythrocyte, which continues through the vertebrate series, is accompanied by an increased concentration of hemoglobin within the corpuscle. This tendency, coupled with an increase in the quantity of corpuscles in the blood, has led to a greater oxygen-carrying capacity in the more highly developed members of the series, and in the more active representatives of the lower groups. In turn the carbon dioxide-combining capacity and buffering powers of the bloods have increased with increasing hemoglobin content.

Throughout the series there has been a tendency for the plasma proteins to increase. This development is probably related to the hydrostatic conditions within the blood vessels and parallels an increase in the blood pressure in the various groups, but it contributes somewhat to the buffer power of the blood. A special tendency of the blood to contain a large quantity of bicarbonate appears in certain of the lower freshwater vertebrates, giving them a specialized type of carbon dioxide dissociation curve.

Throughout the series the respiratory properties of the blood are dependent upon hemoglobin, and the general properties of this substance are displayed in general by all forms. Thus the effect of temperature on the oxygen equilibrium and the buffer action of hemoglobin appear to be very similar throughout. All

hemoglobins, with the exception of that of *Urechis* and under some circumstances the skate, exhibit the remarkable reciprocal relation between oxygen, carbon dioxide, and the products of their reaction with hemoglobin.

Quantitatively, however, there is clear individuality in the behavior of the hemoglobin of the different species. This appears in the shape of the oxygen dissociation curve, particularly in birds and fishes; in the oxygen pressures necessary to cause the hemoglobin to unite with oxygen; in the magnitude of the effect of altered hydrogen ion concentration on these pressures; and reciprocally in the effect of oxygenation and reduction on the quantity of carbon dioxide with which the blood will combine.

To what extent may these developments, quantitative or qualitative, be related to the special physiological problems faced by the respiratory mechanism of the various animals?

PHYSIOLOGICAL CONSIDERATIONS

Early students of the distribution of hemoglobin among the invertebrates were struck with its sporadic occurrence and pointed out that the possessors of this substance were animals which lived in places in which the oxygen supply is limited. It was suggested that hemoglobin developed in response to this situation, and that the substance provided a useful reservoir of oxygen for use in times of need. This suggestion was examined by Miss Leitch (52), who showed that in *Planorbis* the supply of oxygen combined with hemoglobin was only sufficient to last the animal for three minutes and consequently could not be considered seriously as a provision for prolonged anaërobic existence. The oxygen storage theory has been reviewed by Barcroft (6), who pointed out that the oxygen combined with *Arenicola* blood is sufficient to meet the requirements of the worm for an hour or thereabouts and will thus serve to tide over the period when the animal closes its burrow at low water. A somewhat similar situation occurs in *Sipunculus* (12) and *Urechis* (61). In the latter the oxygen content of the blood is sufficient to last about an hour, and probably serves during the prolonged periods of rest when respiratory activity is interrupted.

Borden (10) has re-examined the matter in a careful study of *Planorbis corneus* and *Arenicola marina*. She finds that the blood of *Planorbis* can combine enough oxygen to last 18 minutes and that this together with the air entrapped in the lung is sufficient to enable the snail to endure an hour's subjection to oxygen deficiency. She concluded that in both *Planorbis* and *Arenicola* the function of the hemoglobin is to carry oxygen when the animals are subjected to low oxygen pressures, but that the importance of hemoglobin as a temporary store is not negligible in either species. There can be no doubt that the oxygen capacity of the blood is important in enabling animals to resist short periods of suspended respiration, as in whales and diving birds, but it is significant that high oxygen capacities are developed in those forms which are most dependent on an abundant oxygen supply, as in the pelagic fish, birds, and mammals, and not in those which dwell in poorly aërated regions. Animals which are resistant to oxygen-lack frequently are devoid of respiratory pigment and their resistance appears to depend rather on other qualities of their tissues.

The proper significance of hemoglobin in relation to the oxygen of the environment was clearly shown by the experiments of Miss Leitch on *Planorbis* and

Chironomus. She found that in these forms the hemoglobin is fully oxygenated when the animals are in well-aërated water. Under such circumstances the solubility of oxygen in the body fluids is sufficient to meet all metabolic requirements. It is not until the oxygen pressure in the water has fallen to 50 mm. in *Planorbis*, and 7 mm. in *Chironomus*, that the oxygen combined with the hemoglobin is utilized. These forms are able to live in water poor in oxygen because their hemoglobin will take up oxygen at low pressures and transport it to the tissues. The condition appears to be similar in the earthworm (22) (42) and *Urechis* (61).

Krogh and Leitch (49) have extended this view to explain the pressures at which the blood of fishes combines with oxygen. Using the tension of oxygen at which the blood is half saturated as an index, they pointed out that in fresh-water fishes, such as the carp, eel, and pike, which are occasionally exposed to low oxygen pressures, the tension of half

TABLE 6

Tension of Oxygen at Which Various Bloods Are Half Saturated under Approximately Physiological Conditions

SPECIES	TEMPERATURE	pH	CARBON DIOXIDE PRESSURE	OXYGEN TENSION OF HALF SATURATION
	°C.		mm. Hg	mm. Hg
Planorbis corneus (87)	20		0?	6.0
Arenicola (6)	20	7.3	7.3	1.8
Urechis caupo (61)	19	7.1	7.1	12.0
Siphunculus nudus (30a)	19		0–80	8.0*
Spirographis Spallanzanii (32a)	20	8.0		14.0†
Skate, *Raia ocellata* (20)	10	7.8	1.0	20.0
Mackerel, *Scomber scombrus* (65)	20		1.0	17.0
Sea robin, *Prionotus carolinus* (65)	20		1.0	16.0
Toadfish, *Opsanus tau* (65)	20		1.0	14.0
Cod (49)	15		0?	18.0
Plaice (49)	15		0?	10.0
Trout (49)	17		0?	11.0
Carp (80)	18		30	9.6
Carp (49)	17		0?	2–3
Pike (49)	17		0?	2–3
Eel (49)	17		0?	2–3
Amphiuma tridactyla (67)	26		43	28
Rana esculenta (87)	20		0?	10
Tortoise, *Pseudemys concinna* (70)	25		40	20–30
Snapping turtle, *Chelydra serpentina* (35)	20		42	22
Crocodile, *Crocodilus acutus* (19)	29	7.2		38
Pigeon (81)	42		40	50
Duck (81)	42		40	50
Goose (82)	42		50	37.5
Horse (35)	38	7.46	41	26
Man (35)	38	7.47	41	26
Sea lion, *Eumetopias stelleri* (31)	38		44	40
Porpoise, *Phocaena phocaena* (60)	38	7.25	46	31

* Blood contains hemerythrin.

† Blood contains chlorocruorin.

saturation is comparatively low as compared to marine fish, the cod and plaice, and such fresh-water fish as the trout, which are not normally exposed to very low oxygen tensions. They considered the properties of the blood in both cases to be specially adapted to the biological conditions.

In order that the data which have since accumulated may be considered from this standpoint Table 6 has been prepared. In it are entered the tensions of oxygen at which the bloods of the various species are half saturated under conditions of hydrogen ion concentration, carbon dioxide pressure, and temperature as near to those obtaining in the circulation of the living animal as can be, in view of the available data. The full oxygen dissociation curves for some of the bloods under these conditions are shown in Figs. 1 and 2. So far as the fishes are concerned, the newer data on the marine forms, the skate, mackerel, toadfish, and sea robin, fall within the limits set by the marine forms studied by Krogh and Leitch. *Arenicola* comes up to expectation in having a very low working tension. It is difficult to see, however, why *Urechis* should have a blood working at tensions as high as the trout, or the skate have a blood adapted to higher tensions, when temperature is taken into account, than the mackerel.

When the terrestrial vertebrates are considered, it is apparent that their bloods in general require higher oxygen tensions for half saturation. This fact is due in part no doubt to the higher temperatures at which these animals live, or maintain their body. At first sight one might expect the Amphibia and aquatic reptiles to have blood adapted to working at low tensions of oxygen, in a way similar to the carp and eel, yet this is clearly not the case. In order to properly weigh the data, it must be considered that the properties of the blood determine not only the conditions for the absorption of oxygen at the respiratory surface, but for its discharge from the blood into the tissues. Bloods with oxygen dissociation curves lying at low tensions favor the former and hinder the latter process. In each organism the optimal condition for the blood is a compromise in which these two processes are balanced. The factors determining the properties of the blood most favorable to the respiratory exchange are not only the tension of oxygen in the environment, but the structural and physiological properties of the respiratory organs and the vascular system as well as the general habits of the organism. The complex, and frequently antagonistic nature of these factors makes the teleological argument extremely dangerous, for it is easy to find some aspect of the problem for which the blood is well adapted, at the same time overlooking factors which may work the other way.

The tensions at which the bloods of the amphibians and terrestrial vertebrates combine with oxygen, when contrasted with the fishes, suggest an adaptation directed toward a more rapid and complete exchange of oxygen between the blood and the tissues. In the case of the aquatic reptiles, birds, and mammals, this may be an advantage in allowing the animal to utilize more completely the oxygen combined with the blood during periods when external respiration is interrupted by submergence. It is not clear how this would favor respiration in *Amphiuma*, which presumably absorbs oxygen from the water in which it is submerged. In the warm-blooded vertebrates, with their high metabolic rates, the high tension at which oxygen is held in the blood is of undoubted advantage in facilitating the rapid flow of oxygen from the blood to the tissues. In this way

the properties of the blood of the birds (81) and the sea lion (31) are of advantage.

A different interpretation of these facts has recently been developed (59) from the consideration that the properties of the blood may be related to the characteristics of the atmosphere at the time when the various forms were evolved, rather than to the nature of their present-day environment. If the view postulated by certain geologists, that the quantity of oxygen in the atmosphere has increased since the earlier Paleozoic times, be accepted, it is not unreasonable to expect that the more recent group of animals may possess blood capable of taking advantage of this change. With this view the data here under review are in general accordance.

The relations of carbon dioxide to the oxygen equilibrium are also important and complicate the appraisal of any argument concerning the adaptation of the bloods to respiratory needs. It has been pointed out that the transport of carbon dioxide is dependent in large measure upon the buffer action of hemoglobin and that in most animals the character of the carbon dioxide dissociation curve is related to the quantity of hemoglobin in the blood and hence to its oxygen-carrying power. This is appropriate, for in general the need for transporting carbon dioxide is proportional to the oxygen consumption.

The pressure of carbon dioxide in the blood varies greatly in different animals, depending largely on whether the respiratory organs are gills or lungs. In the case of the fish the blood is exposed to very low tensions of carbon dioxide in traversing the gills, and consequently contains carbon dioxide at pressures which do not appear to exceed a few millimeters (20) (65). The hydrogen ion concentration of the fish blood is consequently lower than that usually observed in other vertebrates. This fact alone tends to cause the blood to combine with oxygen at low tensions and, together with the temperature of the water, accounts in large part for the generally low range of oxygen pressures at which fish blood functions. These factors do not, of course, explain the different characters of the blood of different fishes. Root has pointed out the high sensitivity of the hemoglobin of certain teleosts to carbon dioxide and has suggested that it is adjusted to function in an environment of low carbon dioxide tension, such as the gills offer. This point is of importance in evaluating the properties of the blood of the higher vertebrates. One might equally well say that the blood of fishes is ill adapted to functioning under the higher carbon dioxide pressures to which the blood of all pulmonate vertebrates is exposed and thus stress the adaptive character of the latter.

It has been pointed out that the carbon dioxide dissociation curve of the blood of a number of the lower vertebrates is peculiarly high and flat, owing to the large quantity of bicarbonate present in it. It is difficult to see what purpose is served by this special arrangement, as it can be of no advantage in buffering the blood against carbonic acid. It would, however, enable the animal to care for the accumulation of considerable quantities of non-volatile acid through the elimination of an equivalent quantity of carbon dioxide. It is noteworthy that the animals possessing blood with this character are all fresh-water vertebrates whose habitats or habits submit them from time to time to asphyxial conditions. If this generalization is valid one might expect a similar type of carbon dioxide dissociation curve in the crocodile. This is not the case, however, in the blood of the

crocodile, of which the carbon dioxide dissociation curve is shown in Fig. 6. This blood contained a large quantity of lactic acid which may have decomposed the excess of bicarbonate. The high carbon dioxide capacities of the blood of the alligator observed by Hopping (38) when taken in connection with the accompanying oxygen capacities suggest that this animal also may have a carbon dioxide dissociation curve of the atypical form.

Arguments from the evolutionary and teleological viewpoints are equally treacherous and perhaps are not strictly pertinent to the scientific inquiry into the nature of the respiratory phenomena exhibited by the blood. It is safer and perhaps more valuable to inquire more closely into just what conditions characterize this function in the respiration of the living animal. There are sufficient data to define the conditions existing in the blood throughout the respiratory cycle in a number of animals and these are summarized in Table 7.

TABLE 7

Conditions Existing in the Blood in the Course of the Respiratory Cycle during Inactivity

SPECIES	URECHIS* (61)	SKATE (20)	SNAPPING TURTLE† (35)	DUCK‡ (81)	HORSE (35)	MAN (35)
Temperature, °C.	19	10.4	20	42	37	37
Oxygen capacity, vol. per cent.	4 50	6.00	6.40	17 0	21.4	20 5
Total O_2, vol. per cent:						
Arterial blood	4.1	5.90	5.82	16.6	20.0	19.4
Venous blood		1.98	2.12	6 6	13.5	14 1
Total O_2 transport		3.92	3.70	10 0	6.5	5.3
Saturation, per cent						
Arterial blood	97	93	95	95	98	96
Total CO_2, vol. per cent						
Arterial blood	8.8	7.70	96.43	47	44.9	48 2
Venous blood		10.84	99.39	55	50.3	52.0
Total CO_2 transport, vol. per cent		3.14	2.96	8	5.4	4.2
O_2 tension, mm. Hg						
Arterial blood	75	70	57.0	102	100	78
Venous blood		14	15.0	37	38	40
CO_2 tension, mm. Hg						
Arterial blood	7.2	1.3	38.5	54	41.6	40
Venous blood		2.6	45.2	65	49 2	45 4
CO_2 tension in respiratory organ	5.3	0				39
pH arterial serum	7.1	7.82	7.60		7 43	7.455
pH on becoming venous		−0 15	−0 06		−0.03	−0.026

* Conditions in coelomic fluid entered as arterial blood.

† Blood from lungs entered as arterial blood; blood from tissues entered as venous blood. For conditions in systemic arteries, see Henderson (35).

‡ Mean values from author's data.

In *Urechis*, a large worm of sedentary habit, there is no vascular system. The coelomic fluid, which functions as blood, has a relatively large volume and, although the erythrocytes are not numerous nor rich in hemoglobin, the total oxygen capacity is sufficient to last the animal for about an hour. One cannot distinguish between arterial and venous blood or properly speak of a circulation. The

coelomic fluid is merely churned about through peristaltic movements of the body wall and hind gut, successive portions of it being brought into contact with the active tissues or with the wall of the hind gut which forms the respiratory surface. The latter organ is "ventilated" with fresh water with sufficient regularity to keep more than a third of the oxygen within it from being absorbed. This gives sufficient oxygen pressure to saturate the blood almost completely and since only one-sixtieth of the blood's oxygen is used each minute, the blood as a whole remains so saturated. The coelomic fluid of *Urechis* serves as a reservoir for oxygen, keeping each tissue surrounded by an excessive supply of this gas, rather than as a means of bringing a constant stream of oxygen to the active parts. Carbon dioxide accumulates to a pressure of about five millimeters in the hind gut and consequently carbon dioxide is retained in the blood, but not at pressures greater than 7 millimeters. The coelomic fluid is unbuffered save for hemoglobin and consequently becomes more acid than sea water or the blood of higher forms but does not exceed neutrality.

In the skate anatomical considerations produce a situation in marked contrast. With the presence of a closed circulatory system the blood is concerned solely with *transport* of oxygen. The hemoglobin is well oxygenated in the gills, and in traversing the tissue capillaries gives up two-thirds of its oxygen content. This utilization, large when contrasted with the higher forms, implies a corresponding economy in the rate at which the blood is circulated and correlates with a circulatory system in which the blood must traverse two capillary systems in each circuit. Because of the high degree to which the oxygen is utilized, the pressure of oxygen in the venous blood, and presumably the mean pressure in the capillaries, is low. The pressure-head driving oxygen from blood to tissues must be correspondingly low, but this is tolerated because of the generally low metabolic rate of this inactive fish. In passing the gills the blood is exposed to water of negligible carbon dioxide content. The pressure of carbon dioxide in the blood and its carbon dioxide content are accordingly low and the pH value high. Corresponding to the large utilization of the oxygen in each increment of blood, there is an equally great carbon dioxide transport, relative to the total buffering capacity. The acid base equilibrium is shifted consequently as the arterial blood becomes venous and an unusually large change in pH of the blood results.

The snapping turtle resembles the skate in the fact that the utilization of oxygen is relatively great. In this form also the circulatory mechanism is spared at the expense of the oxygen-transporting power of the blood. The circulatory system is handicapped by the mixing of pulmonary and venous blood in the ventricle, so that the blood in the systemic circulation is not fully oxygenated and has characteristics midway between those listed as "arterial" and "venous" in Table 7. This fact must be important in necessitating the high utilization of the oxygen transport. The turtle's blood is well oxygenated when leaving the lung, although the pressure of oxygen in it is relatively low owing to the incompleteness in the ventilation of the lung. Because of the latter fact and the high degree to which the oxygen in the blood is utilized, the mean pressure of oxygen in the capillaries must be relatively low. The principal difference distinguishing the turtle from the fish consists in the high carbon dioxide tension in both arterial and venous blood, which is a reflection of the carbon dioxide accumu-

lated in the lung and the extraordinarily great total carbon dioxide content due to the atypical character of the carbon dioxide dissociation curve. These factors interact to give a pH value to the arterial blood which is higher than that found in the mammals though not so high as in the blood of the fish.

In the blood of the warm-blooded vertebrates the characteristics of the changes in the respiratory cycle reflect an organization suited to more intense metabolic activity. The oxygen capacity of the blood is much higher and the vascular system of these forms is suited to circulating the blood with greater rapidity and under higher pressure. In spite of the higher metabolic rates of the mammals, sufficient oxygen is supplied to the tissue without the utilization of such a large fraction of the oxygen contained in the blood, a possibility realized by virtue of the higher oxygen capacity and the more rapid rate of circulation. The pressure of oxygen in the venous blood and consequently the mean pressure existing in the capillaries, is maintained at a higher level than that observed in the cold-blooded forms. In this way a high pressure-head is provided for the rapid diffusion of oxygen from the blood to the tissues. The low degree of utilization of the oxygen present in the blood also leaves a larger margin which may be drawn on by the tissues during increased activity. The pressure of carbon dioxide in the blood is high since the ventilation of the mammalian lung is not sufficiently rapid to prevent the considerable accumulation of carbon dioxide in the alveolar air. The blood contains in consequence a high total carbon dioxide content, but as most of this is in the form of bicarbonate, it still retains a distinctly alkaline reaction. It is noteworthy that in the mammals the change in the pH in the blood passing from artery to vein is small compared to the lower forms, reflecting the higher development of the mechanisms for preserving the constancy of its physicochemical state.

The general picture presented by the blood of the duck differs from that observed in the mammals chiefly in the greater extent to which the oxygen circulating in the blood through the capillaries is utilized. It is difficult to be sure that this difference is not due to disturbances in the circulation or respiration incident to the collection of blood samples for analysis, since this was done, in the case of the data recorded for the duck, under anesthesia. However, the shape of the oxygen dissociation curve in the duck is such as to favor a high degree of utilization without corresponding loss in mean capillary oxygen pressure. It is not impossible that the high activities and metabolic rates of birds are facilitated by this character of the oxygen dissociation curve, enabling a greater quantity of oxygen to be transported by the blood and used without increasing the work which the heart must do in circulating the blood.

These cases make it clear that in the evolution of animals a wide variety has arisen in the quantitative aspects of the functioning of the blood in respiration. They depend on the specific properties as well as on the relative proportions of the constituents of the blood, and on the relations which exist between the activity of the animal, the nature of its environment, and the structure and function of its circulatory and respiratory mechanisms. On the whole, the picture is one of a system developing simultaneously in its various parts toward greater efficiency in supplying the requisites for activity, for terrestrial life, and for stability of function in the face of varying need.

In compiling the data presented in this paper it has been necessary frequently to change the units of measurement and carry out other minor mathematical transformations on the figures presented by the authors of the original work. For such changes the writer assumes full responsibility. References should consequently be taken as indicating the source from which the original information was obtained. In the citation of literature no attempt has been made at historical completeness and no attention has been paid to questions of priority as these matters are sufficiently presented in certain of the general papers referred to (1) (4) (5) (16) (30) (35) (64) (86). It has been the endeavor to draw attention rather to the principal recent investigations which contribute to the subject.

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THE EVOLUTION OF BLOOD-FORMING TISSUES

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THE phylogeny of hemopoietic tissues may be traced in a direct line from lower invertebrates to mammals. The attempt accurately to plot this route becomes a fascinating exercise, and the data disclosed provide a highly interesting story. Whether the sequence suggested is closely authentic, as representing faithfully actual evolutionary events, may be considered doubtful at certain points, more especially at that which pertains to the transition from the achordata to the chordata. However, the larger features of the outline, particularly among the vertebrates, may be accepted confidently as substantially in accord with a reasonable interpretation of the facts. At any rate, no real hiatus exists as regards blood and blood-forming tissues between invertebrates and vertebrates. Whether the evolution of blood as between these two groups be regarded as continuous or parallel, the occurrence of erythrocytes and even erythroplastids in the blood of both certain worms and of mammals removes any basis for fundamental distinction in respect of blood. Moreover, lymphocytes and granulocytes, eosinophilic, special and basophilic, occur throughout the metazoa except the very lowest. Also, a peculiar type of spindle cell, a modified lymphocyte, occurs both in certain polychetes (e.g., *Amphitrite*) and in cyclostomes. There are no doubt many instances of parallelism in the evolutionary process. As such may be designated with considerable degree of certainty, the presence of erythrocytes in the annelid and echinoderm phyla; respiratory pigment in the blood plasma of Mollusca and Crustacea; lymphogenous organs in arachnids, Mollusca, Echinoidea and Aves; and the various types of granulocytes among certain classes.

For the purpose in hand it will be essential to adhere closely to what appears to be the main track of evolutionary advance. This may not at all points correspond with the accepted taxonomic order; data concerning blood forming tissues will be considered apart from other phylogenetic data. The temptation to digress along side lines, as among the Mollusca and the Arthropoda, must here be resisted in the interests of simplicity and appropriate space limitations. The direct line of blood evolution leads apparently at the crucial level from segmented worms to cyclostomes. Hematological data give comparatively little support to the hypothesis of the arachnid origin of vertebrates (Patten, '12). The blood of arachnids contains lymphocytes, monocytes, and eosinophils with bacillary granules; but it lacks cells with respiratory pigment. The presence of lymphogenous organs (e.g., the 'gland of Blanchard' in scorpions) suggests a high level of development, but apparently only signifies an instance of parallel evolution.

Respiratory pigment

Before passing to the consideration of blood cells, the location of respiratory pigments should be considered. Where such pigments occur, as among certain worms, holothurians, gastropods, Crustacea, and *Limulus*, whether in the form of hemoglobin, hemerythrin, chlorocruorin,

or hemocyanin, it resides generally in the celomic fluid or the blood plasma. In a few forms among certain worms it is located in cells, apparently modified lymphocytes. It would seem logical to conclude that residence of respiratory pigment in cells represents an evolutionary functional advance over its solution in the plasma. This is the generally accepted interpretation. However, certain facts disclosed by Redfield and Florkin ('31) demonstrate that inclusion of hemoglobin within cells does not among invertebrates necessarily signify a superior oxygen-carrying mechanism as compared with its solution in plasma. They have shown that the bloods of *Arenicola* and *Spirographis*, where the respiratory pigments, hemoglobin and chlorocruorin respectively, are carried in solution in the plasma, have a greater oxygen content than *Urechis* and the other invertebrate forms in which oxygen is transported in hemoglobiniferous cells.

BLOOD FORMING TISSUES OF INVERTEBRATES

Hemocytopoietic tissue makes its first appearance in the lower Metazoa. At the beginning, as exemplified by the sponges, it is represented by lymphocyte-like cells of larger and smaller varieties, and by granulocytes. These cells are ameboid elements within the mesoglea. The so-called lymphocytes have in general the characteristics of the hemocytoblasts of vertebrate forms. They are variously designated as hyaline leukocytes (Kollmann, '08) and amebocytes (Cuénot, '29). The granulocytes are weakly acidophilic. Only slight advance has been effected as far as the flatworms. The blood elements are still diffusely scattered through the middle body layer, except for the small number which have migrated into the primitive vascular system in the Nemertinea.

Beginning with segmented worms a tremendous evolution has been achieved. A series of segmentally arranged leukocytopoietic organs occurs. These organs produce granulocytes and lymphocytes. The hemocytopoietic tissue is the epithelium lining the peritoneal cavity. The arrangement is admirably illustrated in the case of the oligochete, *Pheretima indica*, recently studied by Kindred ('29). The 'blood' cells are essentially celomic elements. Secondarily these cells migrate in part into the blood vascular channels. The blood plasma of annelids contains a respiratory pigment, either hemoglobin or hemerythrin. Among the invertebrates the vascular channels develop independently of their cellular contents. Among the vertebrates also, vasculogenesis and hemocytogenesis are independent processes except in the Amniota during earliest stages, especially in the yolk sac. In the Anamniota the two processes are separate from the beginning. This matter will be discussed below.

In a few aberrant (degenerated or specialized?) annelids, namely the gephyreans and glycerids, blood-cell evolution has approached the limit achieved by the higher vertebrates. Hemoglobin-containing 'erythrocytes' occur (Goodrich, '97; Redfield and Florkin, '31); and in two genera, namely *Thallasema* and *Magelona*, even anucleation takes place (Romieu, '23), producing thus genuine erythroplastids, comparable to the red blood corpuscles of mammals. These erythrocytes are essentially modified lymphocytes. Nothing higher than this is achieved among invertebrates. Only in certain holothurians (e.g., *Thyone*, Van der Heyde, '22; *Cucumaria*, Kindred, '24) do a few hemoglobiniferous cells occur. Kindred suggests that the need for erythrocytes in these forms may be related to the presence of considerable muscle.

Among the Arthropoda and the Mollusca, the respiratory pigment of the blood plasma is hemocyanin, a copper-containing substance. Lymphogenous organs occur throughout these groups. The 'blood' cells are still essentially peritoneal elements. Secondarily they may enter the blood vessels. They include lymphocytes and granulocytes.

The earliest chordata show a decided retrogression, as compared especially with segmented worms. Only in the lowest fishes, the cylostomes, do we encounter a higher degree of development of hemocytopoietic tissue. In *Balanoglossus* and *Amphioxus* blood cells are represented only by a few very primitive amebocytes. The blood of tunicates contains in addition primitive amphophilic granulocytes and cells with variously colored spherules (George, '31).

The subvertebrate chordates, as regards hemocytopoietic tissue, are at about the level of the nemertean worms. If the blood-evolutionary process was continuous from invertebrates to vertebrates, it must apparently be traced from annelids to cyclostomes; and the intermediate groups of the taxonomic order must be considered as representing retrogressions or specialized side branches. All things considered, it seems more in accord with the data to consider blood evolution in vertebrates and invertebrates as a parallel than as a continuous process. However, no real gap exists between vertebrate and invertebrate bloods. Erythrocytes and even erythroplastids occur in both groups; and lymphocytes (hemoblasts; amebocytes) and granulocytes, with closely similar characteristics, occur from sponges to man.

Significance of blood

The primary purpose of blood is tissue respiration. This necessitates the transportation of oxygen. Accordingly, efficient blood must have oxygen-carrying capacity. Under the simple conditions in certain worms the celomic fluid subserves this function in slight degree. Where a simple vascular system has appeared the blood plasma assists or takes predominance in this function. The oxygen-carrying property of these fluids is enhanced by the presence of a respiratory pigment, like hemoglobin. A still more efficient respiratory mechanism is developed with the segregation of the respiratory pigment in certain cells, first of the celomic fluid, secondarily of the blood vessels. The cells available for this purpose are the primitive lymphoid hemoblasts. In annelids these are free peritoneal elements, circulating originally in the celomic fluid. In the vertebrates they are lymphocyte-like cells derived from the reticular stroma enveloping venous sinusoids, whether in spleen or bone marrow. The shift from exclusive splenic erythrocytogenesis to predominant bone-marrow erythrocytogenesis at the level of the Anura may mean largely a gain in bulk of hemopoietic tissue necessitated by an increasing degree of metabolic activity in the transition from cold to warm blooded animals. The shift was made readily possible by reason of the favorable vascular conditions of the marrow, in essential respects closely similar to those of the spleen. The initial purpose of blood vessels was apparently to permit a more intimate circulation of plasma. Cells were only secondarily added, by process of invasion. The vascular system furnishes a ready means for the wide and rapid distribution of granulocytes and phagocytes. At the level of the higher worms, the ancestral leukocytes (lymphoid hemoblasts) became utilized for the elaboration of respiratory pigment in the service of tissue respiration, in the form of erythrocytes.

BLOOD FORMING TISSUES OF VERTEBRATES

Confining further attention to the hemocytopoietic tissue of vertebrates, we encounter most primitive conditions in the hagfish (*Myxine glutinosa*). Among vertebrates the fundamental blood-producing tissue is the mesodermal envelope (submucosa) of the gastro-intestinal canal. In the hagfish this layer contains innumerable masses of actively hemocytopoietic tissue enveloping the venous channels in the form of islets and cords of differentiating blood cells (Jordan and Speidel, '30). This tissue constitutes in fact a disperse spleen (fig. 1). As such it represents the earliest known stage in the phylogeny of the spleen. The spleen is the primary blood-forming organ throughout the vertebrate group.

FIG. 1. TRANSVERSE SECTION OF PORTION OF INTESTINAL WALL OF HAGFISH, INCLUDING ONE LONGITUDINAL FOLD

The core of the fold and the subjacent portion of the tela submucosa show the large irregular patches of splenic (myeloid) tissue enveloping the venous channels. Magnification 25 diameters

The constituent cells of this primitive

spleen are hemoblasts and granuloblasts. The walls of the venous sinusoids are fenestrated. Hemoblasts freely enter the sinusoids. Here the larger hemoblasts differentiate into erythrocytes; the smaller differentiate into spindle cells and thrombocytes. Granuloblasts begin their differentiation only extravascularly; the differentiation may be completed within the circulation. In the hagfish the general circulation is a locus of extensive blood cell proliferation and differentiation.

Conditions in the lamprey are very similar to those in the hagfish, except that a slight advance has been achieved in the evolution of the spleen. The spleen is still diffuse, but not disperse; it is still within the intestinal wall, but aggregated largely within the spiral valve (fig. 2). This hemocytopoietic tissue of the marsipobranchs has the essential characteristics of red bone-marrow. It is virtually myeloid tissue. This identity of splenic, myeloid and lymphoid tissue in the early stages of the evolution of hemocytopoietic tissue is of primary significance. The central fact in this evolutionary process concerns the phylogenetic history of the lymphocyte.

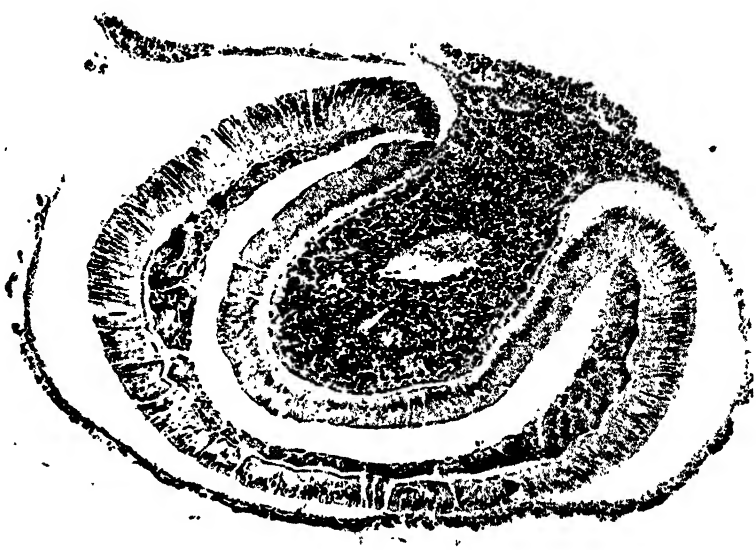

Fig. 2. Transverse Section of Intestine of Lamprey
The hemocytopoietic (splenic) tissue is aggregated in the spiral valve. Magnification 70 diameters

The Dipnoi present the third salient step in the evolution of the spleen (fig. 3). The spleen is still intraenteral, but it is now fairly sharply segregated in the wall of the stomach (Jordan and Speidel, '31). Granulocytopoiesis remains extensive and active in the wall of the intestine. This granulocytopoietic remnant of an originally disperse spleen within the wall of the intestine foreshadows the lymphoid aggregate nodules of the intestine of mammals. It represents further the first step in the future complete separation of the original tripartite condition of the primitive spleen into tissues essentially lymphocytopoi-

etic, granulocytopoietic and erythrocytopoietic.

In ganoids appears the earliest stage of the extraenteral spleen. Here the spleen is a compact, sharply segregated mass of hemocytopoietic tissue, close to the gastro-intestinal junction but topographically distinct and attached to the mesentery. In all of the higher vertebrates the spleen is essentially like that of the ganoids, but spatially somewhat less closely related to the stomach. Ganoids are further peculiar in the possession of a distinct lymphoid organ on the surface of the heart (Drzewina, '05).

Among vertebrates red-cell formation is associated with the presence of a spleen. The sub-vertebrate chordates lack both hemoglobiniferous cells and a spleen. Furthermore, erythrocytopoiesis is associated with a sinusoidal venous circulation. The special condition of a sluggish or relatively stagnant blood current provides the necessary stimulus for hemoglobin elaboration. The specific factor is presumably relatively high carbon dioxide concentration.

It would be expected theoretically that hemocytopoiesis should occur also in the mesonephros. This is actually the case. In ganoids renal hemocytopoiesis is quite

FIG. 3. TRANSVERSE SECTION OF STOMACH OF AFRICAN LUNGFISH
The spleen is embedded in the wall of the stomach. Between the gastric lumen (at left) and the spleen (at right) appears a portion of the pancreas. Magnification 70 diameters.

active, especially granulocytopoiesis. The same is true for elasmobranchs, and more especially for teleosts. It occurs also extensively in larval amphibians. The renal portal system provides the condition favorable for red-cell formation. The sinusoidal venous mechanism of the mesonephros is closely like that of spleen and bone-marrow. Granulocytes differentiate adjacent to the venous channels and subsequently penetrate their walls. Entering lymphoid hemoblasts differentiate into erythrocytes within the venous lumen.

In elasmobranchs a further division of the hemocytopoietic process occurs. Granulocytopoiesis is active in the subcapsular and stromal areas of the gonads. The mother tissue is a primitive connective tissue. This represents a special modification of the hemocytopoietic process in this group. It apparently has no evolutionary significance beyond the fact that sparsely vascularized mesenchyme is a potential locus for granulocytopoiesis.

A similar modification appears in most salamanders. Here granulocytopoiesis is largely restricted to the subcapsular (cortical) region of the liver. In *Proteus anginneus* it is restricted to the intertubular regions of the mesonephros. In *Necturus* this tissue occurs in considerable amount in both liver and mesonephros, and to a slight degree in the epicardium (Dawson, '32). The specific differential condition for granulocytopoiesis seems to be relatively sparse blood supply. The variable extraenteral distribution of loci of granulocytopoiesis in different classes, e.g., in gonads, mesonephroi, liver, bone marrow, appears to have little if any genetic significance. The selection of site for granulocyte differentiation seems to be a matter of adaptation to conditions peculiar to a class (e.g., elasmobranchs) or even a genus. In *Triturus* granulocytopoiesis is practically restricted to the subcapsular region of the liver. But in *Proteus*, conditions resemble those of teleost fishes; the liver is inactive or only slightly active and granulocytopoiesis is practically restricted to the mesonephros. However, in *Necturus* both liver and mesonephros are active. That hepatic granulocytopoietic activity is not closely related to the water-living habit, is indicated by the fact that in the terrestrial salamander, *Plethodon cinereus*, the liver contains a lympho-granulocytopoietic layer like that of *Triturus* and *Amphiuma*.

Hemopoietic conditions in *Proteus anguineus* merit further comment by reason of certain special characteristics. In the first place, lymphocytes are completely absent from the wall of the intestine; lymphocytes are not here lost by migration through the intestinal mucosa. The evidence is exceptionally clear that lymphocytes are lost by transformation into other types of blood cells. In the spleen the larger lymphocytes differentiate only into erythrocytes, the smaller into thrombocytes. Size of cell, or the stage of the distance in terms of number of mitoses from the ancestral lymphoid hemoblast seems to determine whether a cell shall develop hemoglobin and become an erythrocyte or develop thrombogenetic granules and become a thrombocyte. Similarly, in the mesonephros the newly-formed and larger lymphoid hemoblasts develop into eosinophils, the slightly smaller daughter cells of original hemoblasts develop into neutrophils. The evidence from *Proteus* is entirely in accord with the monophyletic theory of blood-cell origin.

In Amphibia we meet with the first appearance of hemocytopoietic bone marrow. In the Anura, as represented by the frog, the marrow of the long bones becomes very active in blood formation during metamorphosis, and annually for a brief period immediately following hi-

bernation. At other times red-cell formation is almost entirely restricted to the spleen. Lymphocytopoiesis is active in the intestine. In the Anura the small, diffuse collections of lymphocytes in the axillary and inguinal regions may foreshadow the future lymph nodes of higher vertebrates. Lymph nodes occur first in birds, and here only in water birds (Further, '13). They consist of two pairs of nodes, one in the neck and one near the kidneys. They are peculiar in that the more compact lymphoid tissue occurs centrally. Typical lymph nodes occur first in Mammalia.

Beginning with Reptilia, the bone marrow assumes a larger rôle in red-cell formation. The spleen remains active, but in lesser degree as we pass through Aves and the lower Mammalia. Among the Mammalia the spleen maintains a considerable adult activity in the opossum, the bat and the hedgehog.

HEMOPOIETIC SEQUENCE IN MAN

Before considering the significance of bone marrow hemocytopoiesis, it seems profitable to compare the ontogenetic history of blood-forming tissues in mammals with the phylogeny just outlined. The first locus of hemocytogenesis in the mammal is the wall of the yolk sac. Immediately after the first appearance of blood islands in the yolk sac, in part coincident with the process in this region, similar hemocytopoietic islands appear in the body stalk of primates. Next, such islands may appear in the body mesenchyme, then in the hepatic stroma. These regions remain active into the early part of the second month of embryonic development.

The hemocytopoietic loci mentioned represent in essence parts of the embryonic gut (fig. 4). This ontogenetic stage of hemocytopoiesis, covering approximately the first five weeks of human development,

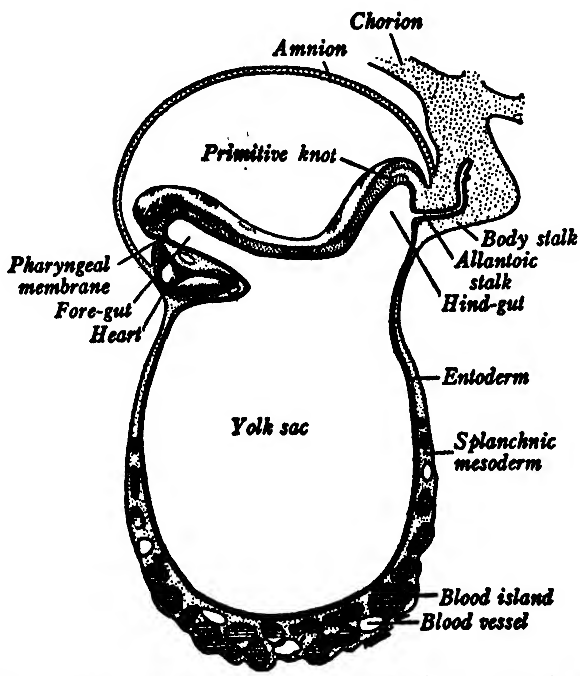

FIG. 4. RECONSTRUCTION OF A HUMAN EMBRYO OF THE FOURTH WEEK (MALL-DANDY) SEEN IN SAGITTAL SECTION After Prentiss and Arey. Magnification 23 diameters

corresponds roughly with the phylogenetic stage represented by the cyclostomes, when the spleen occurs as a disperse intraenteral organ. The gut arises from the vault of the primitive yolk sac. Following the partial separation of the gut from the yolk sac, the latter represents in essence a herniated portion of the intestine. The mesodermal body stalk covers the allantois, an evagination from the yolk sac or gut, thus in essence comparable to the mesodermal covering of the intestine. The primitive body mesenchyme also represents a peri-intestinal layer. The liver primordium is an intestinal evagination; its stromal mesenchyme is comparable to the intestinal submucosa.

For a time after the middle of the second month the hepatic sinusoids of man are a locus of extensive red cell multiplication and differentiation. This stage is comparable to the phylogenetic stage of the teleost fishes.

Towards the end of the second month the spleen begins its hemocytopoietic activity. The spleen develops in the dorsal mesogastrium. This condition is comparable to the phylogenetic stage represented by the lungfish where the spleen remains within the wall of the stomach. The spleen is the predominant erythrocytopoietic organ in fishes and amphibians.

Early in the third month of human development considerable hemocytopoiesis occurs in the mesonephros. Red cells differentiate within the venous channels; granulocytes differentiate extravascularly. In higher fishes and in larval Amphibia, the kidney has a variable but generally considerable hemocytopoietic activity. During the second and third months red cell proliferation and differentiation occur extensively also in the peripheral blood stream. This phase is comparable to similar activity in adult fishes and urodele Amphibia.

Bone marrow makes its appearance in man first during the sixth week, in the clavicles. During the third month bone marrow hemocytopoiesis is active. This stage is comparable to that represented in successively greater degree by reptiles, birds, and mammals.

Lymph nodes appear late in the third month. This ontogenetic stage corresponds with that represented by water birds, where for the first time two pairs of primitive nodes occur.

Significance of spleen

Regarding the spleen as an aggregation of lymphocytes in the mesodermal covering of the gastro-intestinal tract (dorsal mesogastrium), secondarily separated phylogenetically and ontogenetically as a distinct body attached to the mesentery, it appears that this organ is the primary hemocytopoietic tissue. Such interpretation requires explanation of secondary extensive hemocytopoietic activity in the mesonephros, and the predominant blood-forming activity of bone marrow in mammals. It requires further an explanation of the division in phylogeny of the original tripartite function of the spleen, among bone marrow and lymph nodes, with retention of lymphocytopoiesis and the potentiality to produce granulocytes and erythrocytes under certain conditions. The explanation may regard the lymphoid masses of the intestine as phylogenetic remnants of the originally intraenterally placed spleen, retained for purposes in part of supplying ancestors for granulocytes required presumably for antitoxic functions.

It needs to be emphasized that genuine lymphocytes occur in phylogeny long before lymph nodes appear. Genuine lymphocytes occur with the appearance of an aggregate spleen, accordingly first in the lungfish, more abundantly in ganoid and teleost fishes. Their evolu-

tion traces back to the hemocytoblasts of the cyclostome spleen.

The claim of Alder and Huber ('23) that lymphocytes occur for the first time in birds is based upon their failure to differentiate in the blood of amphibians and reptiles between the hemocytoblast and the lymphocyte stages of the lymphoid hemoblast. The hemocytoblasts are in general larger cells with more vesicular nucleus, the chromatin of which occurs in the form of minute granules evenly distributed. The lymphocytes are smaller cells, representing in general division products of hemocytoblasts. Their chromatin occurs in large irregular blocks. The nucleus of both hemocytoblasts and lymphocytes may contain one or several nucleoli. Between the two varieties of lymphoid hemoblasts occur transitional stages with respect to both cell size and nuclear configuration. Since lymphocytes were observed to differentiate into erythrocytes in the blood of amphibians and reptiles, Alder and Huber designated these cells hemocytoblasts. Such interpretation brings the matter in accord with the diphyletic theory of blood-cell origin, but it disregards the true morphology of the red-cell ancestor. The blood of amphibians contains both genuine hemocytoblasts and genuine lymphocytes. But the lymphocytes only represent later stages of differentiation of the hemocytoblasts and develop into erythrocytes in the splenic sinuses and in the circulation.

The essential features of the spleen as concerns red cell formation include lymphocytes and a sinusoidal venous circulation. The lymphocytes, as potential hemocytoblasts, develop into erythrocytes intravascularly, into granulocytes extravascularly. The sinusoidal circulation of the spleen is closely reproduced in liver, mesonephros and bone marrow. Hemocytoblasts (lymphocytes) in any of these locations differentiate into erythrocytes. The combination in these loci of the two fundamental requisite factors for red cell formation, lymphoid hemoblasts and stagnant blood, explains the hemocytopoietic activity.

Significance of bone marrow

Bone marrow arose as a necessary nutritive mechanism for hollow bones. Having the peculiar vascular arrangement requisite for hemocytopoiesis, circulatory hemoblasts aggregate here to further differentiate into erythrocytes. Since the stroma of bone marrow consists of reticular connective tissue, a local source of lymphocytopoiesis is provided. Lymphoid hemoblasts of bone marrow differentiate into granulocytes extravascularly and into erythrocytes intravascularly. Bone marrow hemocytopoiesis is thus, phylogenetically considered, in a sense an accidental matter, incidental to bone development.

Significance of lymph nodes

Can a similar interpretation be placed upon lymph nodes? The answer involves explanation of the function of lymph nodes. The obvious function of lymph nodes is the production of lymphocytes. But this is also a primary function of the spleen, and a partial function of bone marrow. It is clear also that lymph nodes serve as filters on the blood system. Lymph nodes, accordingly, function as accessory blood filters, removing certain deleterious products from the lymph before its mixture with the blood. Moreover, spleen and lymph nodes have an identical reticular stroma, the original source of lymphocytes and macrophages. Only the internal blood and lymph vascular systems are different in spleen and lymph nodes. In the spleen, due to the venous sinusoids, conditions are favorable for red-cell differentiation. Vascular conditions in

lymph nodes normally are unfavorable for such differentiation. Abnormally, as in certain leukemias and anemias, red cell formation may occur in lymph nodes; and granulocytes may arise from lymphocytes both in spleen and lymph nodes.

Lymph nodes, then, would seem to be in a sense accessory spleens, as concerns filtration and lymphocyte and macrophage production. They produce enormous numbers of lymphocytes daily. These lymphocytes enter the blood stream through the large lymphatic ducts. They represent circulatory hemocytoblasts, retaining potentialities for differentiation into erythrocytes, monocytes and granulocytes, depending upon specific environmental stimuli. Aggregating in bone marrow they encounter the proper stimuli leading to erythrocyte differentiation.

Significance of the thymus

The foregoing discussion has included no mention of the thymus. The omission is deliberate and seems warranted in view of the continued disagreement regarding the nature of the parenchyma. If the parenchyma is properly regarded as composed of lymphocytes, then the thymus belongs with the lymphoid organs. As such it is a lymphocyte producer. The local granulocytes are at least in large part immigrant elements. Since the thymus occurs throughout the vertebrate phylum it antedates lymph nodes, and may be regarded as accessory to the spleen in the production of lymphocytes.

THE EVOLUTION OF THE LYMPHOCYTE

The above discussion has involved in fact the evolution of the lymphocyte. Recapitulating this as a distinct subject, we must begin consideration with conditions in the hagfish. Here only lymphoid cells with typical hemocytoblast features occur. Extravascularly these differentiate into granulocytes, intravascularly into erythrocytes, thrombocytes and peculiar fusiform cells. The same is true for the lamprey. Thrombocytes and fusiform cells generally develop only from the smaller hemoblasts.

In the lungfish both typical hemocytoblasts and typical lymphocytes occur in the peripheral blood. Both undergo further differentiation, the larger into erythrocytes, the smaller into thrombocytes. The smallest lymphocytes, with pycnotic nuclei, in both the spleen and the circulation are apparently regressive phases and suffer degeneration. The term *lymphoid hemoblast* is used to designate inclusively hemocytoblasts and the hemogenic lymphocytes.

In ganoid and elasmobranch fishes lymphocytes begin to outnumber the hemocytoblasts in the circulation. The lymphocyte preponderance becomes still greater in teleost fishes. Circulatory hemocytoblasts become successively less numerous through the ascending scale of Urodela, Anura, and Reptilia. The blood of birds and mammals normally contains no hemocytoblasts. These cells are restricted to the central tissues; bone marrow, spleen and lymph nodes.

The lymphocyte represents a slightly more differentiated hemocytoblast. Small lymphocytes are the division products of large lymphocytes. Small lymphocytes may grow to become large lymphocytes. Lymphocytes, except the smallest which degenerate, maintain their ancestral hemocytoblast potentialities to differentiate into granulocytes and erythrocytes. The line of differentiation depends upon the specific environmental stimulus. Apparently, the smaller lymphocytes are produced for the purpose of ready transportation by the blood stream. They are filtered out in large numbers in the bone marrow where they presumably differentiate largely

into erythrocytes. Thus, the venous sinusoids of the bone marrow in the higher vertebrates would seem to subserve the same function as concerns red cell differentiation as does the general circulation in cyclostomes and lungfish and in the mammalian embryo. The lymphocyte, as a blood cell ancestor, has itself undergone evolution during vertebrate phylogeny. The essence of this evolutionary process concerns reduction in size, the results partly of nuclear concentration. The circulating thrombocytes of submammalian vertebrates are the homologues of the stationary megakaryocytes of the bone marrow of mammals.

The phylogenetic source of lymphocytes is the spleen. When lymph nodes become numerous and widely distributed, as in mammals, their lymphocyte products enter the blood stream and aggregate in bone marrow, where the conditions for erythrocyte differentiation are most favorable. The explanation of the origin of lymph nodes, in addition to a spleen, may pertain to their function as phagocyte (monocyte) producers. There is an obvious protective advantage in having these accessory spleens (lymph nodes) widely scattered. These excess lymphocytes may presumably perform their originally splenic function as erythrocyte producers in the bone marrow. Another advantage in the possession of lymph nodes and bone marrow, in addition to a spleen, may inhere in the greater flexibility of such a tripartite mechanism, with the resulting accession of factors of safety in the hemocytopoietic process, and the possibility of compensatory activity for subnormal conditions in any part of the system.

RELATION OF HEMOGENESIS TO VASCULOGENESIS

In young amphibian larvae the future blood-forming tissue is apparently sharply localized, in the form of a 'primitive blood island' in the mid-ventral region of the body between the liver primordium and the anal area. This 'island' has the form of an irregular V-shaped band of cells occupying a space between the entoderm and the ventral splanchnic mesoderm. It becomes visible macroscopically as a darker zone at the stage of development just prior to the beginning of heart pulsation. Frederici ('26) showed that excision of this blood island in embryos of *Rana fusca*, in no way interfered with the normal development of the vascular system; but such embryos lacked red blood cells. These results were confirmed by Goss ('28) for embryos of *Amblystoma punctatum*. Slonimski ('31) has repeated and extended these experiments with embryos of *Rana*, *Amblystoma* and *Bufo*. His results agree with those of Frederici and Goss: The mid-ventral blood island is the sole source of erythrocytes in the amphibian embryo; blood vessels and red blood cells have a different origin; erythrocytes do not arise from endothelium.

This larval blood island of amphibians obviously represents a specialized portion of the primitive submucosa of the gut. As such it is comparable to the spleen of the hagfish. If this comparison is legitimate, then excision of this primordium would necessarily remove all possibility of future development of the spleen and the differentiation of erythrocytes. Independence between vasculogenesis and hemocytogenesis prevails throughout the Metazoa, except in the early embryonic stages of the Amniota. Here, according to the current descriptions, endothelium arises from the peripheral cells of the yolk-sac blood islands, erythrocytes from the central cells. This exception may signify a specialization correlated with an extra-embryonic vascular area associated with a yolk sac. Within the embryonic

body itself, at least after the very earliest stages, vasculogenesis and hemocytogenesis, as in spleen and bone marrow, are again independent processes.

Since the blood vessels of the operated amphibian larvae contain leukocytes, explained as invasions from mesenchymal sources, Slonimski concludes that lymphocytes do not possess the capacity for erythrocyte differentiation; and he rejects the monophyletic interpretation of blood-cell development. However, removal of the primary source of larval erythrocytes, the primitive blood island, may interfere with the respiratory and metabolic needs of the embryo to such a degree as to render impossible the differentiation of lymphocytes into erythrocytes, known to occur in the circulation under normal conditions even in adult stages. Moreover, it must be pointed out that the operated embryos could not be kept alive much beyond a month. If the operated specimens could have been carried beyond the stage of spleen development, assuming that the spleen could differentiate under the conditions of lack of red blood cells even if its primordium had not been removed with the excision of the primitive blood island, the erythrocytopoietic capacity of the splenic lymphocytes might have been able to gain expression. Apparently then, the primitive blood island of amphibians is the sole source of the primitive line of red blood cells. Embryos deprived of this blood-cell primordium are incapable of survival to the time when a differentiated spleen could contribute a second line of erythrocytes and continue as a source for red cell ancestors, namely lymphoid hemoblasts.

SIGNIFICANCE OF RESULTS OF SPLENECTOMY

Splenectomy experiments with amphibia give supplementary information bearing on the phylogenetic sequence of hemocytopoietic tissue. Ablation of the spleen in larval urodeles results in regeneration (Drzewina, '05). In adult urodeles splenectomy results only in shifting erythrocytopoiesis to the general circulation (Jordan and Speidel, '30). Apparently, in the adult the perisplenic mesenchyme is too highly differentiated to serve as potential spleen primordium. In the Anura the results of spleen excision are variable. Frogs either die at about the sixtieth day after splenectomy or they live indefinitely. Those that live have compensated for the loss of the spleen in any one of four different ways. Some produce a new spleen. This result, in the light of conditions in the adult urodeles, must probably be interpreted as a hyperplasia of a microscopic accessory spleen. Some splenectomized frogs develop a hyperplastic marrow in the long bones. This may be interpreted as representing an obligatory utilization of a relatively less favorable, but potentially satisfactory available locus for blood formation. It is comparable to the shift made in evolution at the level of amphibians from splenic to bone marrow erythrocytopoiesis.

Some of the splenectomized frogs compensate by myeloid hyperplasia of the intertubular renal tissue. This represents a backward shift to an ontogenetic larval condition and to a phylogenetic ichthyoid condition. A few of the splenectomized frogs compensate only by myeloid metaplasia of the fat bodies. This result has apparently no phylogenetic significance; it represents utilization of a highly vascularized, structurally potentially favorable, locus for blood cell formation under extreme conditions.

SIMILARITIES OF VASCULAR ARRANGEMENT IN SPLEEN AND BONE MARROW

It may again be recalled that the spleen is the fundamental blood-forming organ in vertebrates. Utilization of bone marrow

is a secondary condition. Possibility of utilization of bone marrow for red cell production inheres in its peculiar vascular mechanism. While developed presumably for optimal bone nutrition, the essential conformity of this vascular mechanism to that of the spleen, made it at once available for the additional function of blood-cell differentiation. The very close similarity in the vascular mechanism of the spleen, from its most primitive condition in the hagfish to its most highly developed form in man, and to that of bone marrow where found, seems of primary significance. The essential matter concerns a structural condition producing a relative blood stasis. The essential structural details concern a rich plexus of venous sinusoidal channels, connecting proximally with long, narrow, non-anastomosing arterial capillaries. The resulting sluggish circulation within the sinusoids is further enhanced by the presence of openings in the endothelial lining providing numerous connections between the vascular lumen and the interstitial spaces of the reticular stroma. The fenestra permit of the ready entrance into the blood stream of extravascular granulocytes and lymphoid hemoblasts. The latter differentiate into erythrocytes within the venous sinuses. In the elaboration of hemoglobin a relatively high carbon dioxide tension is apparently of prime importance.

The splenic vascular arrangement is essentially identical from cyclostomes to mammals. In the hagfish long, straight, narrow capillaries pass from the external surface of the submucosa as branches from longitudinal vessels to the crest of the longitudinal mucous folds. Here they break into sprays of venous vessels which pass in the opposite direction to connect with deep longitudinal submucous veins. Only the venous portions of the vascular mechanism are enveloped with myeloid tissue. This consists of hemocytoblasts and differentiating granulocytes. Both enter the sinusoids for distribution throughout the vascular system. The hemocytoblasts differentiate intravascularly into erythrocytes, spindle cells and thrombocytes. The granulocytes begin their differentiation only extravascularly; the differentiation may be completed within the blood channels.

Conditions in the lamprey are essentially similar. In the spleen of the lungfish, located in the stomach wall, conditions are also closely similar except that granulocyte formation is more active. However, here we have the beginning of the separation of granulocytopoiesis and erythrocytopoiesis. Erythrocytopoiesis occurs only in the spleen; granulocytopoiesis occurs also in the submucosa of the gut throughout its entire extent. At higher levels the separation is maintained, until erythrocytopoiesis and granulocytopoiesis are again associated in the bone marrow of reptiles, birds and mammals. But even here the gut wall maintains considerable lymphocytopoietic and granulocytopoietic activity. The spleen retains practically only lymphocytopoietic activity. The most peculiar form of separation occurs in elasmobranchs where granulocytopoiesis occurs in the gonads; and in urodeles where it occurs in the periphery of the liver (e.g., *Triton*, *Amphiuma*) or in the intertubular stroma of the mesonephros, (e.g., *Proteus*, *Necturus*). All the regions of granulocytopoiesis are characterized by a relatively sparse vascularization.

In the highly developed spleen of mammals the peculiar vascular arrangement seen in cyclostomes is maintained. The nodular arterioles break up into postnodular branches long, straight, non-anastomosing arterioles and arterial capillaries (the sheathed arteries, or penicilli of Ruysch) which connect with a rich

plexus of venous sinusoids with fenestrated walls. This provides for the exit of senile reds and the admission of newly-formed lymphocytes. The lymphocytes do not erythrocytopoietic activity. It appears quite possible that these lymphocytes may be filtered out into the sinuses of the bone marrow in part to differentiate in'o red

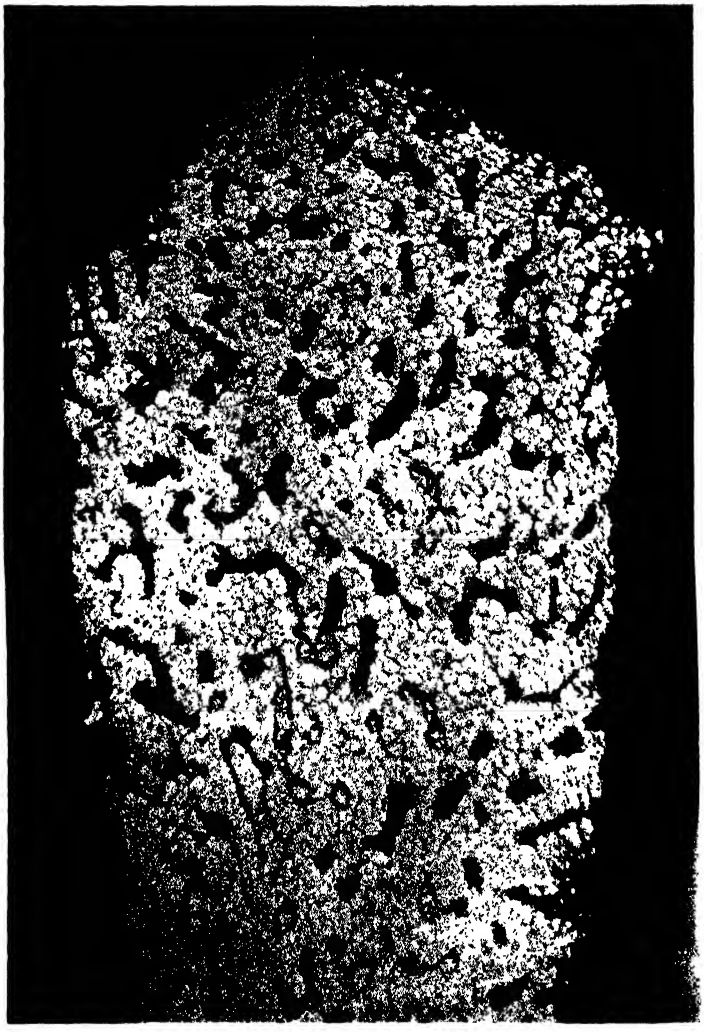

FIG. 5. PHOTOMICROGRAPH OF MEDIAN LONGITUDINAL SECTION OF FEMUR OF A FROG (RANA PIPIENS), SHOWING THE USUAL HYPOPLASTIC CONDITIONS OF THE MARROW, AN EXTENSIVELY VASCULARIZED ADIPOSE TISSUE

Only the venous sinusoids, some filled with blood, can be seen. Hemocytopoetic activity, exclusively granulocytopoetic, is practically limited to the epiphyseal borders and a very narrow discontinuous endosteal area. Magnification, 20 diameters.

normally, after post-fetal life, differentiate into erythrocytes within the circulation. Under certain pathological conditions, however, the spleen may revert to its fetal cells. At any rate the bone marrow has the essential splenic vascular mechanism; one presumably especially adapted for red cell development. The marrow also is

characterized by long, straight, non-anastomosing arterial capillaries, which connect with an abundant venous sinusoidal mechanism. This is especially clearly seen in the normally hypoplastic marrow of the femur of the frog (figs. 5 and 6). Here, again closely recalling conditions in the primitive myeloid spleen of hagfish, the venous channels in slightly hypoplastic marrow are ensheathed with differentiating granulocytes, and typical hemoblasts. Within the sinusoids the hemoblasts, passing through a lymphocyte stage, develop into erythrocytes and spindle cells. The differentiation of lymphoid hemoblasts into erythrocytes in the sluggish circulation in the avian and mammalian spleen and in the bone marrow is closely comparable to this process in the general circulation of fishes and amphibia.

Conclusions

The phylogenetic history of blood-forming tissues clearly indicates the primary importance of the spleen. Renal and bone marrow erythrocytopoiesis are secondary adaptations. The phylogenetic history further demonstrates the erythrocytogenic potentiality of the lymphocyte. The lymphocyte is a later stage of the hemocytoblast; as such it maintains the capacity for elaborating hemoglobin.

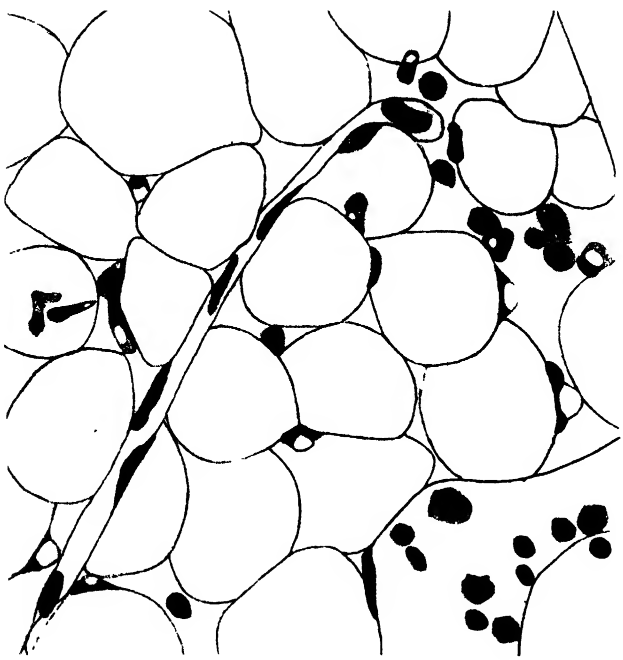

Fig. 6. Small Area of Femoral Marrow (Fig. 5), Showing a Long Arterial (Transition) Capillary to Left of Center; and a Venous Sinusoid with Lymphoid Hemoblasts at Right Lower Portion
From Jordan and Baker, Anat. Rec., vol. 35, 1927. Magnification, 500 diameters

SUMMARY

The direct phylogeny of the blood-forming tissues is obscured by many probable instances of parallel evolution. The less doubtful of these instances may include the elaboration of respiratory pigments among several classes of the invertebrates and all of the vertebrates; the occurrence of lymphogenous organs in segmented worms, gastropods, Crustacea, arachnids

and higher vertebrates; and the presence of similar varieties of granulocytes among the Achordata and the Chordata.

Assuming that the largest number of corresponding features indicates relatively more accurately the direct line of development, the transition from invertebrates to vertebrates, as regards hemogenic tissue, appears to have been made from annelids to cyclostomes. The blood of certain polychetes (e.g., *Amphitrite*) contains peculiar spindle cells, representing morphologically modified lymphocytes. Similar fusiform lymphocytes are found among the vertebrates only in the blood of hagfish and lampreys.

The celomic fluid of gephyreans and glycerids, peculiar worm-like forms generally interpreted as modified annelids, contains genuine erythrocytes similar to those of the blood of vertebrates; and several echiuroid genera (*Thallasema*, *Magelona*) have actual erythroplastids very like the red blood corpuscles of mammals.

Whether the evolution of hemocytopoietic tissue proceeded directly from invertebrates to vertebrates or not, there exists no real gap between the bloods of these larger groups. Apparently identical highly specialized blood cells occur in both groups.

Throughout these groups a lymphocyte-like cell represents the primordial element from which differentiate erythrocytes, granulocytes and monocytes. This primorial blood-cell is originally a peritoneal derivative and constitutes a portion of the cellular content of the celomic fluid. Secondarily, the lymphocytes and their differentiation products may migrate into the primitive vascular channels.

Among the vertebrates this primordial lymphoid hemoblast arises from mesoderm whether in yolk sac, spleen, lymph nodes or bone marrow. Here also in the special blood-forming organs, the spleen and bone marrow, it only becomes a vascular element following migration. Within the venous sinuses it may become transformed into erythrocytes and thrombocytes. Extravascular differentiation leads only to granulocytes; these cells pass through the fenestrated walls of the sinuses at various stages of development.

Beginning with the lowest vertebrates, the hagfish, the evolution of hemocytopoietic tissues presents a relatively clear picture. It involves primarily the spleen as the fundamental blood-forming organ.

In the hagfish the spleen consists of a diffusely scattered, perivenous myeloid tissue throughout the submucosa of the gastro-intestinal tract. In the lamprey the spleen is aggregated within the spiral valve. In the lungfish the spleen is still intraenteral, but no longer diffuse; it has become segregated within the wall of the stomach. The submucosa of the intestine retains considerable granulocytopoietic activity. In ganoid fishes the spleen is a sharply segregated extraenteral myeloid organ attached to the mesentery. In elasmobranchs and teleosts and all of the higher classes the spleen exists essentially as in ganoids. In Amphibia it is still the essential erythrocytopoietic organ. In certain fishes and in larval Amphibia the intertubular tissue of the mesonephros has accessory erythrocytopoietic function.

With the development of long hollow bones, beginning with the Anura, the spleen becomes increasingly less important as an erythrocytopoietic organ. In Aves and Mammalia it is substantially a vestigial organ; blood-formation is here restricted to the bone marrow. The substitution in evolution of bone marrow for spleen as the locus of blood formation finds its explanation in the peculiar vascular mechanism of marrow, and in the relatively larger area and more elastic na-

ture of this tissue. The essential identity between the vascular arrangement of the spleen and bone marrow inheres in the presence of long, straight, non-anastomosing arterial capillaries leading to an extensive system of venous sinusoids. The essential factors for hemoglobin elaboration in these sinusoids are relatively static blood and the consequent high carbon dioxide tension.

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PROBLEMS IN GROWTH CHEMISTRY

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TO THE biochemist, growth means the increase in cell substance, in organic or inorganic cell constituents produced by the organism from food. The capacity of a cell for these compounds is limited, however, and growth will come to an early end unless the cells have also the property to divide. Cell division as such is therefore of paramount importance in the chemistry of growth though we usually think of it more as a cytological problem.

Without the presence of a living cell, the "food compounds" will not change into cells, not even into cell substances. No means has as yet been found to substitute for the cell in this respect. In the following discussion, this capability of the cell to produce cell substances from food will be called "catalysis." No special assumption is made regarding the mechanism of growth catalysts. The expression is used only to differentiate the growth machinery from the building material.

Growth is essentially a chemical synthesis. Cell substances are produced from food which is chemically different from the cell constituents. Synthesis is quite evident with green plants, each of which produces hundreds of different organic compounds from CO_2 plus nitrates and water. But even with carnivorous animals, which eat protein, fat and bones in order to produce protein, fat and bones, a considerable amount of synthesis is accomplished. The architecture of the protein in the cat muscle is quite different from that of the beef muscle from which it may have been built. The food protein is decomposed into small fragments, the amino-acids, by the digestive process, and with these building stones the cat protein is built according to a different style. More convincing still may be the formation of chromosomes of one animal from meat of another animal. A white dog being fed nothing but meat from black dogs, will not turn black. Its chromosomes remain unaffected by the black chromosomes of the food.

This change of food into cell substance is, at least in part, a chemical synthesis, and therefore it requires energy. The necessary amount may not be large, in some cases, but some energy is required. In normally nourished cells, energy is available in liberal amounts. The green plants obtain it from the light, the animals get it from respiration, i.e., from the oxidation of food, and bacteria provide for it by fermentation, which is also a chemical change of the food.

In what form the energy is liberated, and how it is applied in synthesis, we do not know. We may speak of it in terms of calories, but we have no proof that it is produced in form of heat.

OXIDATION-REDUCTION POTENTIALS

A possible explanation presents itself by the conception of potentials as prerequisite for work to be done. A certain minimum pressure is necessary to start a steam engine. It is not the amount of steam, or the size of the boiler that counts. The pressure decides whether or not the engine will run.

The energy liberated in a cell must neces-

sarily establish potentials. One g. of glucose liberates 82 calories when fermented to lactic acid. At the moment when this change takes place, the energy will be limited to the 2 lactic acid molecules just created. This would mean that the lactic acid molecules have a temperature about 82° higher than the rest of the cell (or an energy content in some other form corresponding to this difference of temperature). At the very moment of the splitting of the molecule, the potential difference between the new molecules and the surrounding cell contents is very high. This potential difference is capable of doing work.

Aside from osmotic potentials, the only potential in a cell which we have been able to measure so far, is the oxidation-reduction potential. It indicates the intensity with which a cell can reduce. For example, a certain minimum potential is necessary to reduce methylene blue to the colorless leuco-compound. Most living cells can do that; their reduction potential is strong enough. Only very few bacteria have a potential strong enough to reduce sugar so that hydrogen is developed. The reduction potential in the cells can be tested by injecting indicators.

Whether the reduction potential is used for growth, for synthesis, we do not know. Synthesis is frequently a reduction process, but similar effects are no proof for similar causes.

The reduction potential is brought about by certain compounds which can be oxidized reversibly, and act as oxygen catalysts. Methylene blue is such a substance. It stimulates respiration greatly. To this group belong also the sulphydryl compounds, like cysteine and glutathione, which have been known during the last twenty years to have a decided influence upon cell oxidations.

The presence of any one of these compounds in a solution will give it a definite reduction potential. This does not allow us to predict how much can be reduced or how rapidly, but we can say whether a certain reduction is possible or impossible in this system. For example, in the complete absence of oxygen, methylene blue at pH 6 will be reduced if cysteine is added, but not if glutathione is added (see fig. 1) while at pH 4 and pH 8, both solutions will reduce the dye.

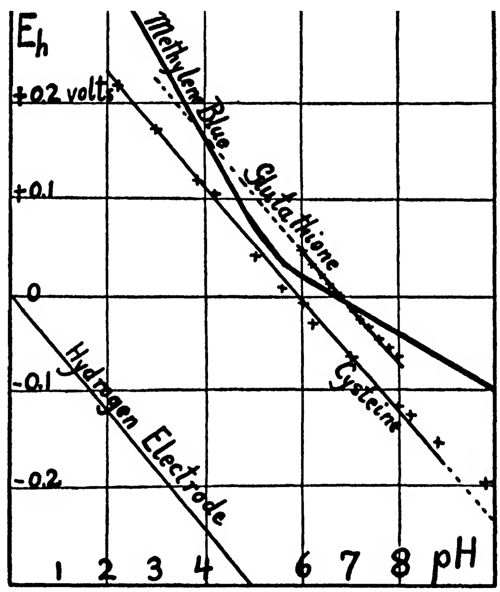


FIG. 1. THE REDUCTION POTENTIALS OF METHYLENE BLUE, GLUTATHIONE AND CYSTEINE, AT DIFFERENT pH, MEASURED IN VOLTS

SULPHYDRYL-COMPOUNDS

For about twenty years, the sulphydryl compounds have been known to be closely connected with the growth problem, as well as with the oxidations in the cell. Recently, Hammett, (1929) has shown them to be even more essential than had been believed before.

He observed that sulphydryl compounds are present in the largest concentration in those tissues where mitosis is most rapid, and within the cell, they are concentrated

in the nucleus. Lead salts which combine with the sulfur of the sulphydryl will prevent mitosis, but do not interfere with an increase of the size of cells. Very dilute solutions of various sulphydryl compounds, containing a few milligrams per liter, will cause a distinctly increased growth rate of plant roots or of paramecium. Quite interesting is the proof that the sulphydryl compounds have nothing to do with the increase in the size of the cell; they stimulate only cell division. Table 1, which is a compilation of parts of two extensive tables by Hammett, shows that sulphydryl compounds increase distinctly the frequency of mitosis, from 12.9 to 17.3 and from 14.7 to 21.5 per cent of all nuclei counted. At the same time, the cells were not enlarged. On the contrary, while the width remained unchanged, the length was shortened by the sulphydryl compounds. There is then a distinct "mitogenetic" effect brought about by the sulphydryl compounds. Ergothioneine, glutathione, insulin and di-thioglycollic acid were also found to give similar results.

The distinction between stimulation of nuclear division on one side and of general assimilative properties, i.e., chemical synthesis and increase in cell size and cell substance on the other side is important.

TABLE 1

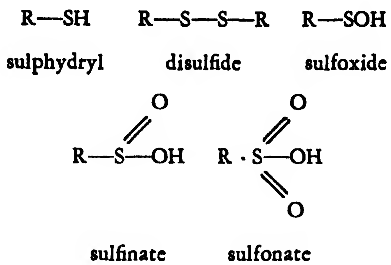
Influence of Thioglycollic Acid and of Cysteine on the Root Growth of Corn (Zea Mays)

NUCLEAR COUNTS, EACH FROM 8 ROOTS						CELL DIMENSIONS			
Total Nuclei		Dividing Nuclei		Percentage of Dividing Nuclei		Average Width of cells in μ		Average Length of cells in μ	
Control	Test	Control	Test	Control	Test	Control	Test	Control	Test
Thioglycollic Acid									
8,014	6,435	756	703	9.4	11.0	14.5	14.2	14.9	14.1
11,274	10,294	1,521	1,790	13.5	17.4	13.7	14.3	14.9	14.1
10,000	8,907	1,523	1,927	15.2	21.6	13.8	14.2	14.8	14.1
11,405	11,540	1,457	2,209	12.8	19.1	14.4	13.8	15.4	13.4
12,332	11,468	1,793	1,947	14.5	17.0	14.9	15.1	15.1	13.9
11,519	11,625	1,342	2,057	11.7	17.7	13.8	13.1	15.2	14.0
Average				12.9%	17.3%	14.2μ	14.1μ	15.1μ	13.9μ
Cysteine									
11,946	10,540	1,756	2,560	14.7	24.3	13.9	14.3	14.3	13.2
10,358	10,608	1,419	2,450	13.7	23.1	14.4	13.4	15.0	14.1
10,007	10,719	1,377	2,125	13.8	19.8	13.8	14.8	15.5	13.9
13,776	12,383	2,256	2,325	16.4	18.8	14.2	13.6	14.7	14.3
Average				14.7%	21.5%	14.1μ	14.0μ	14.9μ	13.9μ

Hammett found the sulphydryl compounds to stimulate cell division in all organisms which he tested; this included some infusoria, (paramecium and ameba), the regeneration of a cut-off foot of the hermit crab, (fig. 2), and the skin of mice.

The partly oxidized sulphydryl compounds, such as sulfoxides and sulfinates, retard growth. Hammett believes that cell division in organisms is regulated by a naturally occurring equilibrium be-

tween sulphydryl compounds and their various oxidation products. The oxidation stages are the following:



Addition of sulphydryl will disturb this equilibrium and produce faster cell division. Addition of partly oxidized sulphydryl will retard cell division.

This is the experimental evidence. Whether the oxidation-reduction potential of the cell will influence this equilibrium, we do not know. It seems probable, but the proof is lacking.

BIOS

In 1901, Wildiers made the observation that in a medium consisting of nothing but mineral salts, sugar, and ammonium salt, yeast will grow only if a large inoculum is used. Small quantities of yeast do not grow (Table 2). If a sufficient number of dead yeast cells is added, growth takes place (Table 3). He concluded that besides sugar, ammonia and minerals, the yeast needed a very small amount of an organic nitrogenous compound for which he suggested the name "bios." He added: "May this word soon be replaced by a chemical term." Today, thirty years later, we are just beginning to replace in part the word "bios."

A surprisingly large amount of work has been done on this problem which is entirely a bacteriological problem. Tanner, in his review (1925) lists 144 papers on bios, and the number has increased considerably since.

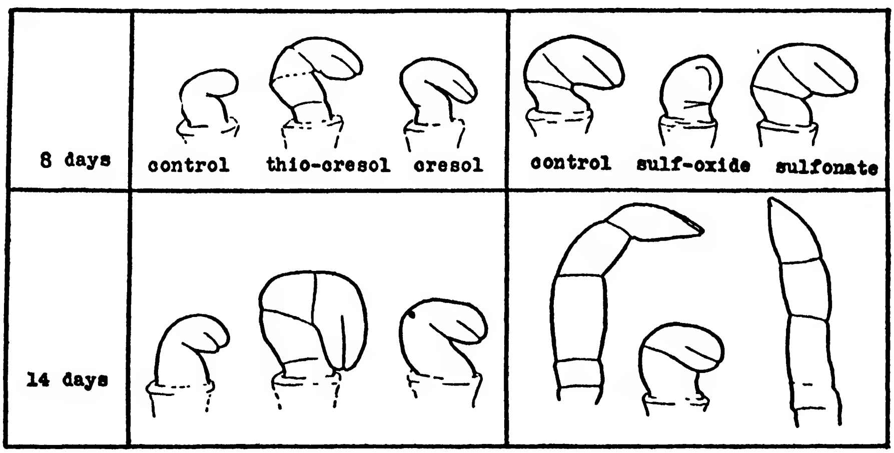


Fig. 2. Regeneration of the First Right Foot of the Hermit Crab (Pagarus longicarpus) in Solutions of Sulphydryl Compounds and Their Oxidation Products

The great confusion, and the many contradictory results obtained by various authors are partly due to different definitions of the term bios. Some authors define it as a compound necessary for growth; there can be no growth without this compound as there is no growth without Ca or K. Others define it as being necessary for "healthy" or "normal" growth, allowing that a poor and slow growth is possible without this compound.

Robertson (1924) found that in a mineral ammonia sugar solution, yeast will grow in the first transfer, and in the successive transfers too, but the growth becomes weaker and weaker, and after about fifteen transfers, ceases altogether. Fulmer and Nelson (1923), however, could keep yeast growing through an unlimited number of transfers in a similar synthetic medium. There are various explanations: there is a great difference in yeasts, even in varieties of the same species. There may have been, in the minerals, lack of an element necessary in very minute quantities. It must be remembered that Hopkins (1930) found that the alga *Chlorella*, for fair growth, requires 0.2 mg. of manganese per liter of solution. This amount was present in several of the c.p. chemicals on the market. If Robertson happened to have chemicals not containing the extremely small amount of some needed element, while Fulmer's chemicals contained it, the different results might be explained.

Miller worked on the other interpretation of bios, on the cause of poor growth in sugar solution + NH_3 + minerals and of good growth when certain substances like meat extract, potato juice, orange or tomato juice, were added in small quantities. One of his associates, Lucas (1924) could separate the accessory food compound into two fractions each of which was inactive while together they increased the crop at least tenfold. One of the fractions has been identified by Eastcott (1928) as inositol $C_6H_{12}O_6$. The other fraction is still unknown.

TABLE 2

Wildiers' Bios. Growth of Yeast (measured by CO_2-Formation) in a Sugar-Mineral Solution + NH_3, with Increasing Amounts of Inoculum (g CO_2 from 125 cc. of culture)

	AMOUNT OF YEAST SUSPENSION ADDED			
	0.25 cc.	1 cc.	2.5 cc.	5 cc.
after 3 days	0	0	0.5	1.9
6	0	0.3	2.2	5.0
8	0.1	1.1	3.9	

TABLE 3

Growth of Yeast (measured by CO_2-formation) in a Sugar-Mineral Solution + NH_3 and + Increasing Amounts of Dead Yeast, from a Small Inoculum of 2 Drops of Suspension (g CO_2 from 125 cc. of culture)

	AMOUNT OF BOILED YEAST SUSPENSION ADDED				
	1 cc.	2 cc.	3 cc.	4 cc.	5 cc.
after 2 days	0	0	0.5	1.2	2.5
3	0	0	1 0	2.1	4.7
4	0	0	1.2	3.0	5.6

Buston and Pramanik (1931) working with the fungus *Nematospora gossypii*, found similar conditions in its growth, and with them, too, one of the fractions contained inositol as the active substance. Reader (1929) working with *Streptothrix corallinus* observed no effects with inositol while mannitol gave much larger crops The concentration used, 0.5 per cent, is s large, however, that the possibility of the mannitol being used merely as source of energy is not entirely excluded. Since

yeasts and fungi are more closely related to each other than to *Streptothrix*, such a difference in response to different compounds is not surprising.

Some authors consider the absence of growth with very small inocula, as shown in tables 2 and 3, to be the real Bios problem. This may be just a case of extreme lag phase.

The lag phase is known to every bacteriologist. It is the period during which old cells transferred to a fresh medium adjust themselves to the new environment. When a culture of yeast or bacteria is transplanted, the cells do not multiply at once. It takes several hours, sometimes even days before the fastest growth rate possible in that medium is reached. During this lag period, the cells change morphologically as well as physiologically. Young, rapidly growing cells, when transferred, show no lag period.

There is one peculiar observation which appears at first to be contrary to expectations. The period of lag increases as the number of transferred cells becomes smaller. This has been observed by a number of bacteriologists, and the best example is probably that by Henrici (1929). He transferred from a yeast suspension decimal dilutions into flasks with sugar-peptone solution, and counted the cells per c.c. in the different cultures at short intervals. Table 4 shows the generation times, i.e., the time required by the yeast cell to double for each interval.

The lag period is the time which elapses before the fastest growth, or the shortest generation time, is reached. If the logarithms of the lag periods are plotted against the decimal dilutions, a good straight line is obtained, from which the lag periods for lower dilutions can be extrapolated, as shown in Table 5. It would take between 4 and 12 days before 2 cells per c.c. would show active growth. This suggests a parallel with the observations by Wildiers (Tables 1 and 2), especially when we consider that Wildiers' medium was less favorable than Henrici's.

TABLE 4

Influence of the size of inoculum upon the duration of the lag period of yeast in a sugar-peptone solution

	SIZE OF INOCULUM IN CELLS PER CC.				
	20,949,750	2,094,975	209,498	20,950	2,095
	Generation Time in Hours				
hours					
0–2	10.8	23.2	23.4		
2–4	*3.0*	4.1	>5.8		
4–6	*3.1*	*1.4*		42.1	
6–8	*2.4*	*1.6*	*1.3*		13.4
8–10	6.9	3.1	*1.1*		
10–12	6.2	2.5	*1.2*	2.7	
12–16	35.5	5.4	2.1	*1.5*	
16–20	301.2	10.6	4.0	*1.1*	20.3
20–24	105.5	46.8	9.2	*1.5*	15.3
24–36	188.5	58.3	75.3	4.6	*2.2*
36–48	668.8	98.8	101.7	50.8	6.3
48–72	>713 0	303.5	163.7	97.9	3.7
72–96		357.5	199.0	517.7	27.9
96–144	2256.0	612.5	1460.0	535.0	2833.3

It does not really matter whether this is what Wildiers meant by Bios. It is one of the growth problems to be solved. Wildiers had observed two handicaps of growth in synthetic media: the failure to grow with small inocula, and a poor yeast crop when no organic food besides sugar was offered. These two phenomena appeared to him as two symptoms of the same cause.

In this he was probably wrong. Lindner (1919) explained the Bios problem, which to him was the lack of growth of small inocula, as an oxygen problem. Yeasts have a tendency to undergo fatty degeneration with oxygen, and thus lose the ability to multiply. In the absence of oxygen, the yeast retains its power to grow in a fresh medium. Several other observations (compiled by Rahn, 1932, p. 202) point in the same direction. This suggests again a connection with the oxidation-reduction potential.

Most organisms have the power to oxidize their food. (The only exceptions are the anaerobic bacteria.) If there is no food, the cells will oxidize their own cell substance. Starving bacteria take up oxygen quite readily, and at a constant rate, (except again the anaerobic bacteria, Callow, 1924). This oxidation of cell substance means injury to the cells.

When the cells are normally nourished, they protect themselves against oxygen by the reduction potential; thus, they can counteract all damage by oxidation. In dry bacteria, lack of moisture inhibits liberation of energy for a potential, and the cells cannot prevent their oxidation. The rate of their death is proportional to the square root of the oxygen concentration (Paul, Birstein and Reuss, 1910).

Single isolated cells transferred to a new medium may have difficulty in establishing a reduction potential against the intruding oxygen, when they are old, and not ready to start operations at once. With a large seeding, the oxygen dissolved in the new medium is divided between many cells, and cells close to each other will have a better chance to establish normal working conditions. After a certain time, the medium itself will have a reduction potential which will relieve even the weakest cells from their paralysis by the oxygen.

The relation between lag and reduction potential is supported by the observation that cysteine enables anaerobes to grow without protection against oxygen. Cysteine is known to establish a reduction potential (see fig. 1).

TABLE 5

The lag period in Table 4 is passed

Observed:		
with an inoculum of	20,949,750 cells in	2–8 hours
with an inoculum of	2,094,975 cells in	4–8 hours
with an inoculum of	209,498 cells in	6–12 hours
with an inoculum of	20,950 cells in	12–24 hours
with an inoculum of	2,095 cells in	24–36 hours
Extrapolated:		
with an inoculum of	209 cells in	2–3 days
with an inoculum of	21 cells in	2.5–6 days
with an inoculum of	2 cells in	4–12 days

VITAMINS

Wildiers made his observations before vitamins had been discovered. It was only natural that afterwards, a good num-

ber of investigators thought that bios must be identical with vitamins. To this analogy dates back the attempt to measure the vitamin B content of foods by their effect upon yeast growth. It was ultimately found that though yeasts benefit greatly by products rich in vitamin, no quantitative parallelism could be established.

We now believe that most bacteria and yeasts can produce their own vitamins. While thus, the vitamin problem does not exist for the bacteriologist, nor for the botanist, it is a very vital one for the animal physiologist. He still searches for a final answer to the question why vitamins are necessary, and how they can act in the extremely minute quantities in which they are efficient.

The vitamin problem is the one of the growth problems with which all biologists are familiar. It needs only to be stated that they are essential for animal life, especially for growth, but also for repair, because the grown animal may also suffer from avitaminoses.

Two vitamins B and D have recently been obtained as pure substances, chemically well defined, and were found to be relatively simple substances, if compared with the molecule of enzymes, the smallest of which is thirty times that of the vitamin. Vitamin A is also known to have a molecular weight of only about 300.

HORMONES

The hormones are secretions of the glands of animals. Their presence or absence determines the normal and abnormal functioning of various parts of the body. The tasks of the hormones are quite specialized, and do not really belong to the general growth problem. They are, as far as they are known, relatively simple compounds.

Some twenty years ago, the German botanist Haberland found a hormone in plants. Wounds in plants would not heal easily if they were washed thoroughly, but if crushed plant cells were put on the wound, it would heal promptly. The healing factor was not destroyed by heat and Haberland, therefore, called it a hormone. Healing in most cases means a multiplication of cells, i.e., growth of cells which had already gone into a resting stage. The wound hormone is therefore a growth activator inducing the division of cells which would not do this without

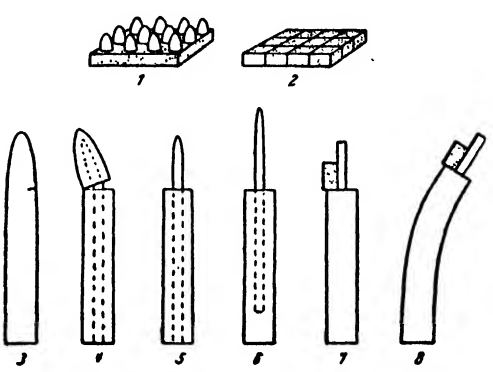


FIG. 3. METHOD OF OBTAINING AND DOSING THE "AUXIN"

1) agar block with 12 tips of coleoptiles; 2) same, after removal of tips, cut in cubes; 3) coleoptile with incision; 4) and 5) decapitation of coleoptile; 6) the first leaf is partly pulled out; 7) after decapitation of first leaf, the agar block is placed on the coleoptile; 8) one-sided growth and bending through one-sided growth stimulation.

the catalyst. The hormone causes a "mitogenetic," i.e., a mitosis-producing effect.

At about the same time, Boysen-Jensen observed a compound inducing growth of the tips of young plants; much later, some Dutch botanists realized the importance of this observation for the general growth problem (Went, 1931). The technique involved is relatively simple, and has become entirely standardized for quantitative work (see fig. 3). The coleoptile of an oat seedling is decapitated, the inner

leaf is partly pulled out, and also decapitated. This stops growth almost completely. If the tip is put back, the coleoptile starts to grow again. The compound causing growth will diffuse into agar, and if the agar is then put on top of the de-

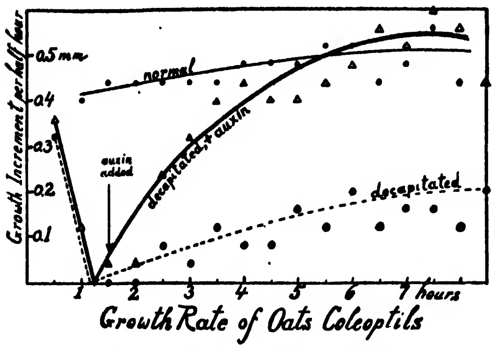


FIG. 4. GROWTH RATES OF COLEOPTILES, NORMAL, DECAPITATED, AND DECAPITATED WITH ADDITION OF AUXIN

capitated coleoptile, it will grow again. If it is placed on one side of the stump, only this side will grow and cause a bending. The angle is used as a measure of the quantity of the growth compound.

TABLE 6

Occurrence of Auxin, the Growth Compound of Coleoptiles, in Nature measured in Avena-Units

	AVENA UNITS
Diffusion product from corn seedling tips	about 300
Rhizopus reflexus	40–110
Bakers yeast	30– 40
Bacterium coli	about 50
Human feces	5–10
Human urine	about 400

This compound is a non-specific growth accelerator; it affects corn and oats as well as English daisies, and is found commonly in nature, as may be seen from Table 6.

The compound which the Dutch botanists call "auxin" has a molecular weight of about 350. It contains no P, N, or S, and is an acid soluble in ether (Kögle and Smit, 1931).

While it is claimed that there is no plant growth without this growth substance, it has not seemed so certain that it causes cell divisions. It seems that the main task of this compound is to cause a stretching of the cells.

THE RÔLE OF THE VARIOUS GROWTH COMPOUNDS

A number of compounds have been mentioned which are essential either for cell division, or for the increase in organic cell substance, i.e., for synthesis, or for growth generally. All these compounds, as far as they are chemically known, are relatively simple compounds, substances of the order of magnitude of sugar molecules (Table 7). This is surprising, for the catalysts of organic destructive processes, the enzymes, have a molecular weight of the order 10,000; they are nearly as large as protein molecules.

Frequently, the vitamins, hormones and similar compounds have been considered to be catalytic agents in the growth process. The small size of the molecule would not necessarily contradict their catalytic nature, but it opens new perspectives; it makes it appear possible that all these compounds may be only building stones for cell construction. Food serves largely as source of energy, and only a small part of it is used as building stones, as e.g., the amino acids.

Very small quantities of certain food substances, a fraction of a milligram of vitamin per person, or 1.7 mg. inositol per liter of medium, for yeast growth, or 0.2 mg. of manganese per liter of medium for algae, decide between life and death. It seems possible, that of certain special molecules in the cell, only very small quantities are needed for construction. The cell contains the nucleus with the

chromosomes which again contain the genes. Each gene is believed to be the carrier, or catalyst, for a certain cell property; consequently, each gene must be chemically different from all other genes. A gene is a very small unit, probably not larger than a very large protein molecule with a molecular weight of about 5,000,000 and a diameter of 24 mμ. Certainly, it is smaller than 100 mμ, for it is below the limit of microscopic visibility. If a special compound, e.g., inositol, should be needed to build one certain gene, it will require only one or a few molecules per cell to accomplish this. The question arises: Are there enough molecules in the extremely small amount needed to provide all cells with sufficient molecules?

This question can be answered, since the weight of molecules is known. For example, with inositol, one gram contains $\frac{6.06 \cdot 10^{23}}{180}$ molecules, because the molecular weight of inositol is 180. According to Eastcott (1928), 0.0167 mg. of inositol will permit the growth of 325,000,000 yeast cells.

0.0167 mg. inositol = $5.62 \cdot 10^{16}$ molecules. This leaves for each cell $\frac{5.62 \cdot 10^{16}}{325{,}000{,}000}$ = $1.7 \cdot 10^{8}$ molecules of inositol.

All inositol of the solution was used; no further growth was possible in the exhausted medium, after addition of sugar. The inositol had not been used for respiration; it could be obtained again quantitatively by boiling the yeast crop with HCl.

As another example, the relation of vitamins to the human body may be computed. Vitamins A, B, and C have a molecular weight of 251 to 382. The average of 300 will be used for this calculation. One g. of vitamin consists of $\frac{6.06 \cdot 10^{23}}{300}$ molecules; that makes $2.02 \cdot 10^{18}$ molecules per mg. The number of cells in

TABLE 7

Molecular weights

NITROGEN-FREE COMPOUNDS FROM ORGANISMS		NITROGENOUS COMPOUNDS FROM ORGANISMS	
acetic acid, $C_2H_4O_2$	60	urea, $CH_4O_2N_2$	60
oxalic acid, $C_2H_2O_4$	90	glycin, $C_2H_5O_2N$	72
lactic acid, $C_3H_6O_3$	90	leucin, $C_6H_{13}O_2N$	131
tartaric acid, $C_4H_6O_6$	150	tyrosin, $C_9H_{11}O_3N$	157
glucose, $C_6H_{12}O_6$	180	cystein, $C_3H_6O_2NS$	106
sucrose, lactose, maltose, $C_{12}H_{22}O_{11}$	342	glutathione	243
fat (tri-stearin) $C_{57}H_{110}O_6$	890	egg albumin	34,500
HORMONES		hemoglobin	68,000
adrenalin, $C_9H_{13}O_3N$	183	serum globulin	103,000
thyroxin, $C_{15}H_{11}ONI_4$	729	legumin	208,000
bios II (inositol)	180	hemocyanin (*Limulus*)	1,760,000
auxin of coleoptiles	330–352	hemocyanin (*Helix*)	5,005,000
VITAMINS		ENZYMES	
vitamin A	about 300	pepsin	39,000
vitamin B_1 (Windaus, Tschesche *et al.*)	251	rennet	11,200
vitamin D_1 and D_2 (Windaus, Lutteringhaus *et al.*)	382	invertase	19,600
		emulsin	37,700

the human body can be estimated only to the order of magnitude. It is essential that the estimate be not too small, and it seems safe to assume that the average body cell is not larger than the red blood corpuscles. These may be considered as cylinders, 2μ high, and with a diameter of 7.5μ, which results in a volume of $88.5\mu^3 = 88.5 \cdot 10^{-12}$ cm.^{3}, or about $90 \cdot 10^{-12}$ g. This would amount to $800 \cdot 10^{12}$ cells for a human body of 75 kg, and this estimate is certainly too large because a good share of the body does not consist of cells. One mg. of vitamin, with $2.02 \cdot 10^{18}$ molecules, would allow $\frac{2.02 \times 10^{18}}{800 \times 10^{12}}$ = about 2,400 molecules per cell.

With yeast, practically all the cells had grown during the experiment with inositol. With vitamins, only the *new* cells would need the construction material, and also those which have to replace deteriorated cell substance. This latter amount can be estimated from the nitrogen loss during inanition to be not more than 1 per cent of the total weight daily. To provide each deteriorating cell of a grown person with one molecule of vitamin, 4×10^{-6} mg. would be needed daily.

While with inositol, there can be little doubt that it is a building stone for the yeast cell, there is no such proof with vitamins. It is a possibility, but it is also imaginable that the vitamins act really as catalysts, and not as building stones.

The same computation can be carried out for the various sulphydryl compounds. However, the situation seems to be different because we are not dealing with increase in cell substance, but only with the mitogenetic effect.

The growth compound of the coleoptiles probably belongs in the same group as the vitamins and the inositol. It is interesting to realize that only the tips of the coleoptiles can produce this substance while the rest of the plant appears to be unable to do so.

Whether hormones, generally, are just building material for the cell, seems rather doubtful, because in many instances, their function is not connected with cell division or increase in cell substance. It is imaginable that a new building material thrown into the blood stream, may be used to change the composition of certain groups of cells and thus make them function differently. But there is no experimental basis for such assumption. It is also imaginable that some hormones are building material while others act catalytically.

MITOGENETIC RADIATION

An entirely different viewpoint on the growth problem was offered by Gurwitsch, a Russian histologist who came to the theoretical conclusion that cell division must be excited by radiation. He proved this in 1923 by letting the radiation from one onion root fall on another onion root. The number of dividing nuclei in the exposed part of the root was much larger than on the opposite side.

The radiation goes through quartz, and thin cellophane, but not through glass nor gelatin, and belongs to the short ultraviolet, of about 2000 Å wave length. The same effect can be produced by the corresponding wave lengths of artificial light.

The original cumbersome method of counting the dividing nuclei in onion roots has since 1928 (Baron) been replaced by counting the percentage of buds on yeast. Yeast is spread over the surface of an agar block, and is then exposed to the biological radiation while a similar block is held under the same conditions, but unexposed, as control. After a definite time, the buds on the yeast cells are counted. This method does not appeal to the bacteriologist, because the percentage of budding

cells is no accurate measure of the growth rate, but it is entirely sufficient to prove whether or not the growth rate has been accelerated by radiation. The radiation is extremely weak. The photographic plate and the ordinary photo-electric cells do not register this radiation. The only physical instrument sufficiently sensitive for this radiation is the Geiger-Mueller counter modified for these wave lengths (Rajewsky, 1931).

It has been shown by Siebert (1928) and by Magrou (1931) that chemical processes may produce the same kind of radiation: the oxidation of glucose with permanganate or peroxide, the oxidation of pyrogallic acid, and the peptic digestion of protein.

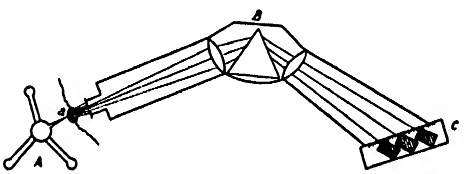


Fig. 5. Technique of Measuring Biological Spectra

A: Stand holding a frog sartorius, (*a*), excited electrically. *B:* quartz prism and quartz lenses of the spectrograph. *C:* glass plate, graduated according to wave lengths; on this glass plate are placed the agar blocks with the yeast.

In Gurwitsch's latest book (1932), the spectral analysis of various biological radiations is given. The radiation is sent through a quartz prism, and the spectrum is analyzed by a series of agar blocks with yeast, in place of the photographic plate (fig. 5).

It has been found that all oxidation processes give the same spectrum, and all proteolytic processes give another characteristic spectrum. The best studied spectrum is that of "glycolysis," i.e., the anaerobic decomposition of sugar. The spectra of glycolysis in blood, of alcoholic and lactic fermentation gave identical lines (fig. 6). The spectrum of the excited muscle does not check with any of these three spectra, but has some other lines besides. All of these spectra or radiations stimulate the growth rate of yeast.

If cells can radiate, and can also be affected by such radiation, then microorganisms in a solution must influence each other. This so-called "muto-radiation" has been studied by Baron (1930) with yeast. He found that with many cells in a drop of good nutrient medium, the percentage of budding cells is larger than with a smaller number of cells. In the latter case, they are too far apart, and the radiation from each cell is largely absorbed before reaching the other cells (Table 8).

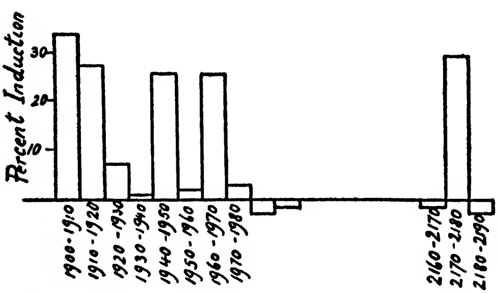


Fig. 6. The Spectrum of Glycolytic Radiation

To prove his point more clearly, Baron added gelatin to the medium. Gelatin absorbs these short wave lengths completely. The result was that even with large numbers per drop, the growth rate was not stimulated; it was the same as with a smaller inoculum (Table 9). All radiation was absorbed before it could reach other cells.

The explanation for extreme lag with very small seedings, as in the cases mentioned in Tables 2 and 3, is very simple. If Gurwitsch's theory is correct that a stimulus of ultra-violet light is needed to induce mitosis, a single cell in a medium can divide only if such radiation comes from outside.

This relation between the amount of inoculum and the length of lag has been explained above by the reduction potential. This suggests the question whether there is a relation between mitogenetic radiation and reduction potential. This does not seem very probable. The energy from cell radiation could hardly be of any account in the energy balance of a yeast cell which decomposes about 50,000,000 molecules of sugar per second (Rahn, 1932, p. 259). But it might be that it is the *form* of energy that counts, and that this special radiation might act like the spark in the powder barrel. The cell may be an amplifier for just this wave length.

Haberland, who discovered the wound hormone in plants, tested whether mitogenetic radiation would heal wounds. No effect was found at all while the contents of crushed cells caused normal healing. Gurwitsch stated thereupon that the chemical compounds were necessary for healing, but that they alone would produce no mitoses unless there was mitogenetic radiation at the same time. This is possible, but it can hardly be proved since all pulp from crushed plants radiates.

TABLE 8

Growth Acceleration by Mutual Irradiation with Saccharomyces ellipsoideus

INOCULUM	NUMBER OF BUDS PER 100 CELLS			
	Experiment No. 1		Experiment No. 2	
	8,000 cells	80,000 cells	8,000 cells	80,000 cells
start	0	0	0	0
after 3 hours	0	0	0	0
after 5 hours	3	16		
after 6 hours			5	49
after 7 hours	14	60		
after 10 hours			17	91
after 12 hours			35	91

TABLE 9

Prevention of Growth Acceleration by Absorbing the Mitogenetic Rays by means of Gelatin

INOCULUM	NUMBER OF BUDS PER 100 CELLS			
	Experiment A		Experiment B	
	8,000 cells	80,000 cells	8,000 cells	80,000 cells
start	1	0	0	0
after 3 hours	2	2	0	0
after 5 hours	18	21	12	15
after 7 hours	30	32		
after 8 hours			35	33
after 10 hours	41	42	48	52
after 12 hours			62	61

CONCLUSIONS

These are the outstanding attempts to understand the chemistry of growth. If

we could correlate all of them and explain one by the other, we could probably discover that there are many other factors still involved. But we cannot even correlate all the facts just mentioned.

Nevertheless, we can speculate about their interrelations, and some of these appear rather simple, though they may not be true.

It has been recently shown by the London biochemical school that vitamins A and B radiate, sufficiently to blacken the photographic plate in 3 days. This is suggestive, but we are far from having proved that vitamins act through their radiations.

The sulphydryl compounds, which are important for growth and which, according to Hammett, regulate the growth rate, have also a great effect upon the reduction potential. But there is no proof that this potential is essential for growth.

The bios of the bacteriologist may be nothing but the establishment of a reduction potential, and may thus link with Hammett's sulphydryl compounds. Some other facts about bios can be best accounted for by mutual irradiation of microörganisms. However, certain experimental facts prove also the need of definite chemical compounds in minute quantities for cell construction.

The auxin of the Dutch botanists stands a little outside of the discussion. It does not seem to be the cause of cell multiplication. It brings about the stretching of the cells, and is therefore necessary for growth; besides it, however, there must be still the "mitogenetic" effect, either chemical or physical.

The necessity of ultra-violet radiation for cell mitosis cannot be considered as proved. All proof so far has shown only the stimulation of the growth rate by such radiation. Unquestionably, the physical effect can be only part of the growth process since the most outstanding indication of growth is chemical synthesis which requires chemical reactions.

Rather surprising is the observation that the outstanding chemical substances in cell synthesis are relatively simple compounds while the agents of digestion and energy supply are from 10 to 100 times as large. The enzymes are of the order of magnitude of simple protein molecules while the hormones, vitamins, sulphydryl compounds, bios and auxin, have a molecular weight similar to that of sugar.

This simplicity suggests that at least some of these compounds may be nothing but building stones for the cells which are needed in very small quantity, but are nevertheless absolutely indispensable, and cannot be manufactured by the cell itself. It is also possible, however, that these compounds may act as catalysts to bring about necessary chemical reactions in the cell.

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THE PROGRESSION FACTOR IN INSECT GROWTH

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THE general curve of growth has been often discussed in recent literature. The present paper will deal only with the discontinuous and abrupt growth of the Arthropoda, as demonstrated in insects. The historical development of the problem has been reviewed by Calvert and Bodenheimer.

The main result of these studies is the verification of Przibram's growth factor. Studying the growth of *Sphodromantis viridis*, he found a quotient of 2 for the weight of every stage as divided by the preceding one. For length, the same quotient proved to be 1.26 ($=\sqrt[3]{2}$). Adding some earlier data on Crustacea (by Brooks, and others) to these results, Przibram felt justified in stating these quotients to be a general rule in the growth of Arthropoda. Bodenheimer extended these studies to all insect orders. His researches showed that in very frequent cases between two moults, there might be two or more doublings of body weight. These non-manifested divisions had been called "latent divisions." Such latent divisions had been found in the growth of Orthoptera, Odonata, and Rhynchota. The Phasmid *Carausius morosus* (Eidmann) may serve as example (see Table 1).

The number of the latent divisions increases considerably in the holometabolic insects. The Tenthredinidid *Cimbex 4-maculata* (Bodenheimer) is here taken as an illustration (see Table 2).

A further increase of latent divisions between the actual moultings may obscure the progression factor. The weight of the Giallo Vittorio race of *Bombyx mori* increases as shown in Table 3.

But if we consider the whole series from the primitive cases like *Carausius* up to the most complicated like *Bombyx*, it will be readily understood that the latter are only deviations from Przibram's principle.

The average quotient for 92 series of quotients for the progression in growth of length was exactly 1.265. A similar series for the progression in weight-growth is represented in Table 4.

It will be seen that the average quotient for all these series is exactly 2.005. The deviations from 2 disappear, if we take the + and − signs into consideration. The table starts with cases like that of *Sphodromantis* and *Toxoptera*, in which each calculated division coincides with an actual moult. In *Carausius* and *Schistocerca* we find one latent division in each. These interpositions have the result that the weights for one or two stages fall between these calculated values. But agreement between the other parts of the series and the calculated data could not be explained without Przibram's principle. The same is true for the more complicated cases.

An interesting discovery in the course of these researches was the fact that the females of nearly all Acrididae, Phasmidae, and probably also Mantidae, doubled their weight between the last moult and the beginning of the oviposition period. As the total weight of the mature ovaria is only one-third of this increase, we must regard the pre-oviposi-

tion period as an additional development stage, which is lacking in the males of these orders.

The agreement with Przibram's factor is obvious. Alpatov (1927) substantiated the same conclusion on *Drosophila*. But

TABLE 1

Observed body weight (in mgs.)	3.6		11	25	50	110	230	480	1,008
Calculated body weight	3.6	7.2	14.7	28.8	57.6	115.2	230.4	460.8	926.2
Observed body length (in mms.)	15.5	22.8		29.5	38.7	51.0	64.7	80.9	
Calculated body length	15.8	20.0	25.3	31.9	40.3	50.9	64.2	80.9	

TABLE 2

Observed body weight (in mgs.)	3.5	7.0	—	39	—	140	—	448	903
Calculated body weight	3.2	7.5	15	29	57	113	226	452	903
Observed body length (in mms.)	7.0	12.3		18.5	—		—	36 0	
Calculated body length	7 0	11.2	14.2	18.0	22.7		28 6	36 0	

TABLE 3

Observed (in mgs.)	0.52	—	—	—	7.4	—	43	—	—	200.1	—	977 6	—	4,100
Calculated	0.5	1	2	4	8	16	32	64	128	256	512	1,025	2,050	4,100

TABLE 4

SPECIES	NUMBER OF MOULTS	NUMBER OF DIVISIONS	ABSOLUTE GROWTH	AVERAGE QUOTIENT OF WEIGHT INCREASE
Sphodromantis viridis	9	9 (10?)	540 (1,080?)	2.03
Carausius morosus	6	7	278	1.98
Schistocerca gregaria	5	7	126	1.90
Dociostaurus maroccanus	5	7	77	1.76
Toxoptera graminum	4	4	16	2.01
Bombyx mori: Giallo Vittorio	4	13	7,884	2.23
Bombyx mori: Nipponoshiki, Gen. 1st.	4	13	8,417	2.11
Bombyx mori: Nipponoshiki, Gen. 2nd.	4	12	3,615	1.87
Bombyx mori: Chan Toung	3	12	5,005	1.97
Philosamia ricini: India	4	10	1,091	2.03
Philosamia ricini: Palestine	4	12	4,843	1.98
Pieris brassicae	4	10	1,024	1.97
	5	10	782	2.11
Dytiscus marginalis	2	6	52	1.87
Epilachna chrysomelina	3	5–6	177	1.98
Apis mellifica	—	11	1,576	2.22
Cimbex 4-maculata	4	8	258	2.05
Average				2.005

Some additional material from recent publications may be discussed. The growth factor of some Odonata (Calvert) is as shown in Table 5.

nevertheless the principle has again and again been misunderstood. Two typical cases from recent publications may be quoted. Larson in studying the

TABLE 5

SPECIES	ACTUAL	CALCULATED	GROWTH QUOTIENT
Lestes viridis	9	12	1.227
Agrion pulchellum	9	9	1.263
Anax junius	13	15	1.253
Pantala flavescens (Honolulu)	10	13	1.272
Pantala flavescens (Philadelphia)	9	10	1.272
Sympetrum vicinum	10	10	1.247
Nannothemis bella	12	12	1.253
Average			1.263

TABLE 6

OBSERVED DATA	CALCULATED DATA	DEVIATION	QUOTIENT	REMARKS
Breadth of Head in mms.				
		per cent		
1.010	.958	+5.4		
1.346	1.207	—	1.33	
	1.521			One latent division
1.807	1.917	−5.6	1.34	
2.407	2.435	−1.1	1.33	
3.068	3.068	+0.0	1.27	
Breadth of Body in mms.				
1.238	1.247	−0.7		
	1.571		1.45	
1.793	1.979	—	1.42	
2.541	2.494	+1.9		Two latent divisions
	3.143	—	1.42	
3.616	3.961			
4 991	4.991	+0.0	1.38	

TABLE 7

AT 20°C.			AT 25°C.		
Observed	Calculated	Deviation	Observed	Calculated	Deviation
		per cent			*per cent*
2.3	1.8	—	2.3	2.1	+9.5
	3.5			4.2	
	6.9			8.4	
13.1	13.9	+5.8	16.5	16.8	−1.8
	27.9			33.6	
60.9	55.9	−10.0	87.2	67.2	
	111.7			134.4	
223.4	223.4	+0	268.8	268.8	+0

growth of *Notonecta glauca* concludes that his quotients do not agree with our conclusions. As a matter of fact, they do agree well enough (see Table 6). These data fully agree with earlier results (Bodenheimer) and confirm that in the linear growth of Heteroptera there are always one or two latent divisions.

For the Japanese Beetle (*Popillia japonica*), Ludwig denies the value of Przibram's principle. But his data mainly confirm it, if we consider that *Popillia* as a holometabolic insect with many divisions cannot show a full agreement. The body weight (in mgs.) after the different moultings is as shown in Table 7.

It would be unreasonable to expect to find that in every case of insect growth the quotients follow our rule. But the comparison of all analyses, which are present in the literature, allows one to draw the conclusion that insect growth in the more primitive conditions of Hemimetabola follows a progression factor of 2 or $n \cdot 2$ in the growth of weight and of $\sqrt[3]{2} = 1.26$ or $n \cdot 1.26$ in the growth of length. It is the increase of latent divisions which obscures these relations somewhat. But even here Przibram's principle is valid.

One misunderstanding, finally, must be removed, this having often been enunciated in literature on the subject. Przibram, Bodenheimer and others are believed to assume that each division is accompanied or even provoked by a contemporaneous division of all body cells. This may be the case and the recent statements of von Buddenbrock that insect moulting is induced by hormones may point in this direction. But no definite statement or special research in this respect has ever been made.

SUMMARY

Insect growth follows a progression factor of 2 or $n \cdot 2$ for weight, and of $\sqrt[3]{2} = 1.26$ or $n \cdot 1.26$ for length. The increase of latent divisions in the Holometabola obscures these relations, without invalidating them.

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Further literature is quoted in (2), (3), (5), (9).

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

AMERICA TODAY AND MAYBE TOMORROW

Being a review of *Recent Social Trends in the United States. Report of the President's Research Committee on Social Trends.* 2 vols. New York (McGraw-Hill Book Co.), 1933. Pp. xcv + 1568. $6\frac{3}{16}$ x $9\frac{1}{4}$. $10.00.

By Raymond Pearl, Department of Biology, School of Hygiene and Public Health, Johns Hopkins University.

I

The presidency of Woodrow Wilson marked the turn of an era in American life in more ways than one. We have been regaled in recent years with a series of books about the pleasanter aspects of living in the "decades" immediately preceding the coming of Mr. Wilson and the World War. These treatises have made clear by sharp contrast the changes and innovations which have necessitated new adjustments and adaptations by the human organism. But one thing that developed in Mr. Wilson's administration, and for which he was in no small measure personally responsible, has either been overlooked entirely by social and political philosophers, or its significance has been somewhat less than adequately apprehended.

I refer to the beginning of the Era of the University Professor as an Important Person in Public Affairs. Up to the time of Mr. Wilson's ascent to the throne university professors were almost universally thought of, if at all, by Really Important People in the United States as "those —— damned professors." But by the middle of 1917 all that had been changed. Great men were being bossed by professors, and liking it. The professor had at long last come into his own in this great republic, and was not only having a grand time, but making it clear to everyone that he was by no means such a silly fool as he had been supposed to be. And he is not only still holding the place so gained but marching onward and upward on this same pathway. To be sure neither Mr. Harding nor Mr. Coolidge showed any particular comprehension of what academic people could do for them. But after all they, each in his own way, were so busily occupied with their personal affairs, again of a totally different kind in each case, that they quite pardonably could not be expected to take a broad view about the utility and importance of the professoriate. And also it must not be forgotten that Mr. Hoover was in the cabinets of both. From the very beginning of his career he has fully appreciated the value of scholarly learning, and drawn unstintingly upon the potentialities of its possessors to further his enterprises, both private and public. Doubtless some day a diligent seeker for the adornment of a Ph.D. will make a proper statistical analysis of the total personnel of the various commissions set up by and through Mr. Hoover alone since April 1917. When this is done the truth of what has been said above will be proven by a documentation overwhelming in its magnitude and appositeness.

The process still goes on. According to what we read in the papers Mr. Roosevelt

needs and heeds the advice of a professor about almost, if not quite, everything he does. Before his administration is six weeks old it may be confidently expected that his henchman, the redoubtable Louisiana Kingfish, will be taking his orders from a dean, or conceivably even a mere assistant professor.

All this is, in the highest degree, commendable from the point of view of the nation's affairs, and that viewpoint alone is our concern at the moment. In the long run we may expect to benefit as England, France, and Germany—indeed every European country I can think of except Russia and perhaps such small fry as Portugal—have benefited for generations by holding learned men in adequate esteem in human affairs generally. There is, of course, another and potentially sadder aspect of the matter. It remains still to be seen how the American professor will bear the spiritual prosperity which inheres in the burgeoning of His Era. The advancement of learning has been generally regarded as the primary business of the university professor. What will be the ultimate effect upon this really difficult and time consuming task of gaily barging into politics, theology, business, and front pages generally? The answer is not yet of record, but, as I have already said, this matter is not our present concern.

II

The processes of natural growth and development of professorial influence in public affairs which have been inadequately outlined above have now in the last days of the Hoover administration reached their highest point. In September, 1929, Mr. Hoover asked "a group of eminent scientists" to tell him whether a survey of social trends in the United States could be made. The answer was so immediate and reassuring that in December of the same year he was able to appoint a Committee consisting of five professors and one officer of a foundation to do the job. The chairman was Dr. Wesley C. Mitchell, easily the ablest and most distinguished American scholar in the so-called social sciences. Steam for the research was generated by a "grant of funds." The Committee of six called to their aid in the task, for one purpose or another, 20 "federal departments and bureaus;" over 100 "research bureaus and organizations," including Kiwanis International, Otis Elevator Company, Women's National Republican Club, and Zonta International, among others more conventionally identified with research enterprises; and so many individuals that merely to list their names and institutions required over 13 pages of close-set print. Of these individuals the vast majority belong in the upper levels of the college and university hierarchy. Here, as never before, the professoriate got a chance to come to grip *en masse* with the great realities of life in troubled times.

The results of this prodigious activity are now before us, having been released on the Monday following last New Year's day. That is to say 202.34 cubic inches (measured unbound) or just a pint short of two gallons, at least, of the results are now available, according to measurements and calculations laboriously made by Reginald the Office Boy. They are to be supplemented at leisure by 13 more volumes of monographs giving additional data to support and extend the conclusions reached in the Report itself. The two volumes of the Report contain a total of 1663 pages, divided into 29 chapters. Four of these chapters emanated from three members of the original Committee (two by Ogburn, and one each by Merriam and Odum). The remaining twenty-five chapters were written by rather more than the same number of persons of repute in the various fields discussed, drawn mainly from universities, and to a relatively much smaller extent from public and private research and welfare organizations of various sorts. In a few cases the men selected by the Committee for the tasks were literally and beyond argument or question the foremost living authorities in their respective fields. In some other cases they quite as clearly could by no stretch of the imagination be regarded as occupying any such position in the opinion of their professional colleagues. But after all somebody had to be chosen to do the work, and somebody had to do the choosing. It would have been a major miracle and something really to worry about if the six who

were responsible for the choosing had turned out to be wholly devoid of human and academic and scholarly prejudices and jealousies; or had been wholly unaware that they themselves were the appointees of a particular person of a certain station in life. Of the six members of the original Committee two are professors in the University of Chicago, one in Columbia University, one in the University of North Carolina, one in Harvard, and one not in academic life. Twenty of the 29 chapters of the report have as sole or part authors university or college men (not counting the persons designated as "with the assistance of"). There were 26 such authors (counting each individual every time he appears). In this list of authors the University of Chicago appears 9 times, Columbia 3 times, University of North Carolina 3 times, Harvard once (total to here 16). Yale contributed one chapter with two joint authors, and the remaining 8 authors each represent a different university or college.

These authors have produced a sound, workmanlike job. A tremendous mass of statistical and other data is digested and made handily available to students in these volumes. While in every chapter I have examined with care there are points made that are open to argument and about which competent students may disagree, there can be no doubt that this report will stand for some time as a useful reference work. A few of the chapters are masterpieces; notably those by O. E. Baker and Edgar Sydenstricker. A technical criticism that can be made of the report as a reference work is that the index is unworthy of the content. There is no author index at all, and no names appear in the subject index. Furthermore the subject index by no means conforms to the highest standards of modern scientific indexing.

III

What of the soul of *Recent Social Trends*, now that we have seen something of its anatomy and embryology? The answer is that it gives a wide-ranging and detailed picture of certain aspects of the United States as it is today, painstakingly painted in durable and quiet tones, calculated on the whole to soothe rather than excite the observer, and with touchy topics either omitted or treated as the Best People would wish them to be. According to the index "socialism" is mentioned on but one page out of 1663. There it is coupled with "fascism," "sovietism," and "trade unionism," and we are told that the American public has "remained relatively docile" in regard to such matters.

It seems improbable that anyone is ever going to get angry over these volumes, or alternatively to burst into paeans of praise about them to his neighbors. But after all the object of the enterprise was not to stimulate but first to describe and then perhaps guide, or prophesy, or both. As a description of the American scene as the Committee sees it today, the volumes are meticulously accurate. If one were to venture upon any general criticism of a work so well-intended and painstakingly wrought as this is, it would perhaps first include some regret at the nearly complete absence of comparative discussion and appraisal. After all, other countries and societies are older than ours and have accumulated a body of experience about their own ups and downs possibly useful in interpreting our own. Anatomists long ago learned that a description of the human body, however detailed and precise, yielded a much inferior understanding of its anatomy than was obtainable when its structures were compared with those of other animals. Indeed it is only in this way that any real insight into the meaning of human anatomy has come.

Another matter deserving of mention is the effect upon the end-product of the manner of its preparation. Apparently with the purpose of making the final report "sound" in the sense of containing nothing to which anyone could take exception, the several chapters—at least a great many if not all of them—were sent for criticism and suggestion to various people supposed in each case to know something about the subject under discussion. At first glance such a plan seems highly commendable. It appears to safeguard against anything like intellectual arrogance and such-like sins. But the method nevertheless has serious drawbacks. It obviously tends to reduce the whole performance to that dead-level of inoffen-

sive intellectual mediocrity which characterizes a departmental bluebook or census report. Anything like an original idea has small chance of survival in such a scheme. The matter is syllogistic, in this way: (1) Any new idea different from the prevailing mode of thought is presumed not "sound" because offensive to the opinions of "sound" authorities; (2) A chapter (and constructively a book) contains one or more new—that is, different—ideas; (3) Therefore that chapter (or book) is not "sound" in its present form and must be altered until it is. In short, above everything else, the manner of thinking and writing characteristic of such men as William Graham Sumner and Vilfredo Pareto (neither of whom, so far as I have been able to discover in the absence of a name index, is mentioned in these volumes) is to be avoided like a pestilence. The technique of a Calvin Coolidge is safer and "sounder."

It seems to me that the consequences of this mode of reasoning are evident in not a few of the chapters, though happily not in all.

IV

Just because it is chiefly a picture of our present day world *Recent Social Trends* inevitably and immediately calls into the reader's mind a comparison with another book, less than one-fourth as long, published some five years ago. I refer to *Les États Unis d'aujourd'hui* by André Siegfried. This was a book written for the purpose of describing the American scene realistically as it exists. It too indulged in a bit of modest prophecy. In short M. Siegfried and the President's Committee aimed at precisely the same target. There is not the smallest doubt that the former sunk his steel-jacketed bullets in the very center of the bullseye. Competent judges all over the world examined the target after he was through shooting and agreed with substantial unanimity about his score. In the literal and precise sense of the words *Les États Unis d'aujourd'hui* attracted worldwide attention and deeply influenced serious public opinion relative to the United States, in all countries of the world except the United States. It was translated into the languages of virtually all civilized peoples. Factually sound and thorough but never pedantic, it penetrated with an almost uncanny insight into the very bowels of American life, and lured the unwearied reader on to its ultimate page by the charm of its style, the vigor and sweep of its reasoning, and the readiness of its wit and good humor. This remarkable book was written by one professor (French) who received, to the best of my knowledge, no "generous grant of funds" whatever to spur him to the task.

As I have already pointed out, and must again emphasize, there is a remarkable parallelism, in respect of their aims, between *Recent Social Trends* and *Les États Unis d'aujourd'hui*. The marksmanship achieved by the two books is, however, singularly different.

Perhaps when M. Siegfried reads this report—as he surely will—he will be reminded of the plaintive remark of Dr. Johnson's old school-mate, who met him again many years later when the learned Doctor was under full head of pontifical steam. "Doctor," he is reported to have said, "I have often tried to become a philosopher, but cheerfulness will keep breaking in."

V

It has been mentioned above that besides its primary descriptive object the President's Committee felt constrained to prophesy or to be constructive when, as, and if the circumstances so moved them. It is upon this aspect of the effort that I wish next to focus attention. Not all of the authors appear to have experienced this urge. But a good many did. Direct quotation seems to be the most effective method here. Unfortunately such quotation must be brief, and consequently cannot do full justice in all cases to the several authors' arguments. Insofar as this is so I tender my apologies in advance. Some of the quotations gain in significance if read aloud slowly, and the implications of all should be pondered over.

Old John Smith, Taxpayer, will be cheered by the following prospects:

> The development of the new super-city points, therefore, to the need of some sort of super-metropolitan government. (p. 496.)
>
> A coherent and active policy as regards the con-

sumer does not exist throughout the government bureaus in Washington at the present time. Historically this has its roots in a long tradition of focusing attention upon the productive forces of the nation, of identifying consumer welfare with business prosperity, and of over-dependence upon the rational adequacy of the consumer's unaided choices. Whether something resembling a Department of the Consumer in Washington, coordinate in budget and power with the strongest of the present departments, is indicated is a secondary question. (p. 911.)

The state may be expected to increase rather than diminish its contributions [to the promotion of the arts] even in days of financial stringency. (p. 1007.)

More specifically, the work of governmental [health] agencies will probably grow, and these agencies, confronted with real needs for therapeutic treatment not being provided elsewhere, will probably give more attention to the function of treatment. (p. 1110.)

Also, the prospect is that the federal government will extend its criminal jurisdiction because of the increasing importance of the interstate aspects of many crimes. (p. 1166.)

The trend which is most important in marking the probable future developments in social welfare is the absorption of activities as a part of public administration in increasing numbers and at an accelerated rate. (p. 1222.)

Technically, the emerging needs appear to be: (1) a more adequate public relief, adapted in principle and methods to meet the demands of social change and emergency and economic cycles and depression; (2) the development of a plan for social insurance which will guarantee security and eliminate more and more the strain of social hazards and fear; and (3) social planning which will bring to bear the fullest utilization of social science and social research and their application through social work and public administration. (p. 1271.)

One factor which should operate to reduce the present burden of taxation is the decline in the general price level. In appraising the strength of this factor, however, it must be remembered that over 50 per cent of all taxes are expended for salaries, wages, and pensions. . . . . Approximately a quarter of the country's tax collections are expended for interest and redemption of indebtedness. (p. 1389.)

Those who believe that the government ought to help them in their efforts to curtail the pleasures of people of whom they do not approve will derive renewed hope and courage from the following:

Another problem of a different kind is the devising of ways and means of better governmental supervision and control of commercial amusements. This involves suitable measures of control over motion pictures and radio broadcasting, and the regulation of dance halls, pool and billiard rooms, cabarets and roadhouses, burlesque theatres, horse racing and other forms of amusement provided on the commercial basis. (p. 956.)

Subtle and profound thinking, and penetrating logic delight every intelligent man. Here is a morsel for his delectation:

Increased divorce is due to the weakening of the functions which served to hold the family together, and no doubt of public opinion, which would appear to be correlated with the exercise of these functions. If, say, six of these eight functions or bonds are weakened, then more divorce is to be expected, unless there is a corresponding strengthening of the other two. The future stability of the family will depend much more on the strength of the affectional bonds. (p. 708.)

Finally the *Social Trends* symphony, after developments, variations, recapitulations, and so on, returns at the end to the keynote. And how this will please everyone who admires the principles of liberty and the rights of man upon which the government of the United States was founded, and which were so carefully embodied in its Constitution by the founding fathers!

If all this seems speculative, we may turn to the development of governmental art in the period of the World War. Under the stress of a national emergency the government responded with surprising energy and efficiency. The subordination of private to public interest, the facility in recruitment of the necessary talent when the boycott on governmental service was lifted, the indifference to established precedent in administrative or other method, the freedom from hair-splitting judicial restraint, the unification of leadership, while not without its disadvantages and abuses as in the unnecessary suppression of freedom of speech, left an abiding impression of the possibilities of governmental reorganization in America, when unified social ideals and symbolism found free expression in public action. (p. 1539.)

VI

In the end, after considerable study and cogitation over these two large volumes, I come reluctantly to the conclusion that William Graham Sumner has himself become a "forgotten man." For in Section 102 of *Folkways* he stated, with devastating clarity and finality, the fallacy underlying such enterprises as seeing "where social stresses are occurring and where major efforts should be undertaken to deal with them constructively," which is what Mr. Hoover says in his foreword that *Recent Social Trends* should help us all to do. Section 102 is too long to quote in full here, I regret to say, but perhaps the following passage will suffice, and with it I am content to end this discussion:

When, however, the statesmen and social philosophers stand ready to undertake any manipulation of institutions and mores, and proceed on the assumption that they can obtain data upon which to proceed with

confidence in that undertaking, as an architect or engineer would obtain data and apply his devices to a task in his art, a fallacy is included which is radical and mischievous beyond measure. We have as yet, no calculus for the variable elements which enter into social problems and no analysis which can unravel their complications. The discussions always reveal the dominion of the prepossessions in the minds of the disputants which are in the mores. We know that an observer of nature always has to know his own personal equation. The mores are a societal equation. When the mores are the thing studied in one's own society, there is an operation like begging the question. . . . . It is vain to imagine that a "scientific man" can divest himself of prejudice or previous opinion, and put himself in an attitude of neutral independence towards the mores. He might as well try to get out of gravity or the pressure of the atmosphere. The most learned scholar reveals all the philistinism and prejudices of the man-on-the-curbstone when mores are in discussion. The most elaborate discussion only consists in revolving on one's own axis. One only finds again the prepossessions which he brought to the consideration of the subject, returned to him with a little more intense faith.

BRIEF NOTICES

EVOLUTION

EVOLUTIONIST AND MISSIONARY JOHN THOMAS GULICK. *Portrayed Through Documents and Discussions.*

By Addison Gulick. University of Chicago Press, Chicago. $4.00. 6x9; xvi + 556; 1932.

The material in this book falls into three parts: I. Youth and Early Travels; II. Productive Life; III. The Biological Evolutionist. The material is derived mainly from personal journals and letters, and family letters. It is skilfully edited and makes altogether an extremely interesting book. One gets first the colorful tale of early missionary activity in the South Seas; and learns, by the way, of the manner of the founding of some of the great Hawaiian fortunes. Then follows the story of *Wanderjahren* in pursuit of an education. Then the life as missionary, culminating in the years in Japan, with their profound and appreciated results. All along is the never ending struggle with ill health and the equally unfailing zeal for natural history. Altogether it was a great life, nobly lived.

After a summary but excellent analysis of Gulick's contributions to evolution, and their significance, the book ends with a bibliography, briefer than one would have supposed to have been the fact, and an index of 40 pages.

Altogether this is a notable contribution to biographical literature, and to the history of biology.

THE SCIENTIFIC BASIS OF EVOLUTION.

By Thomas H. Morgan. W. W. Norton and Co., New York. $3.50. $5\frac{5}{8}$ x $8\frac{1}{2}$; ix + 286; 1932.

In this book one of the foremost living geneticists considers the bearing of modern work in genetics on the problem of evolution. The author's viewpoint is indicated in the following passage:

It is, in fact, the main purpose of this book to insist that the study of evolution has become sufficiently advanced to rest our case for its acceptance on the same scientific procedure that has led to the great advances in chemistry and physics. Whether this procedure is called mechanistic or by some other name does not so much matter as does the recognition that only by experiment may we hope to rescue the theory of evolution from the vague speculative methods of its immediate past. It is mainly for this reason that I have in the last two chapters discussed the opinions of philosophers, metaphysicians, and mystics concerning organic evolution. My contention is that these speculations have not been helpful in finding out how evolution has come about. On the contrary, I think that these attempts to remove the problem from the biological field have done more harm than good, by their popular appeal to mysticism, and by directing attention away from the more laborious but safe procedure of studying the problem of evolution in the same way that other scientific problems are studied.

THE CAUSES OF EVOLUTION.

By J. B. S. Haldane. Harper and Bros., New York. $2.50. $5\frac{1}{4}$ x $7\frac{3}{4}$; vii + 235; 1932.

In this book the author summarizes the genetic evidence on variation and interspecific differences and the work of Fisher, Wright and himself on the mathematical theory of natural selection. His conclusion is

that natural selection is the main cause of evolutionary change in species as a whole. But the actual steps by which individuals come to differ from their parents are due to causes other than selection, and in consequence evolution can only follow certain paths. These paths are determined by factors which we can only very dimly conjecture. Only a thorough-going study of variation will lighten our darkness. Although we have found reason to differ from Darwin

on many points, it appears that he was commonly right when he thought for himself, but often wrong when he took the prevailing views of his time—on heredity, for example—for granted.

A Chronological Table of Prehistory. *By Miles Burkitt and V. Gordon Childe. Roland Austin, 24 Parkend Road, Gloucester, England.* 2s. 6d. $7\frac{1}{8} \times 9\frac{3}{4}$; 22 + folding chart; 1932 (paper).

All the established facts from Eolithic times up to Julius Caesar and Roman times, are presented in tabular form. The tabular chart is divided into twenty-eight columns headed by geographical areas, covering the known prehistoric world. There is a twenty-ninth column headed "Climatic phases." These columns are divided on the vertical axes into Eolithic, Lower Palaeolithic, Middle Palaeolithic, and Upper Palaeolithic periods, followed by the calendar dates 3000 B.C. to 0, in approximately 200 year intervals. A brief discussion of prehistory accompanies and supplements the table.

Altogether the chart gives a sound and well-correlated picture of the stratigraphy of man's cultural evolution.

Contributions to Paleontology from Carnegie Institution of Washington. *Papers Concerning the Palaeontology of California, Oregon and the Northern Great Basin Province. Carnegie Institution of Washington Publication No. 418.*

Carnegie Institution of Washington. $2.00 (paper); $3.00 (cloth). $6\frac{3}{4} \times 10$; 113; 1932.

This monograph contains six descriptive papers: I. Distribution and Age of Marine Tertiary Deposits of the Colorado Desert, by W. P. Woodring; II. Distribution and Description of Skull Remains of the Pliocene Antelope *Spenophalos* from the Northern Great Basin Province, by Eustace L. Furlong; III. A Miocene Mammalian Fauna from Southeastern Oregon, by C. Lewis Gazin; IV. Additions to the Mammalian Fauna from the Tecuya Beds, California, by Chester Stock; V. A New Genus of Otter from the Pliocene of the Northern Great Basin Province, by Eustace L. Furlong; and VI. A Contribution to the Paleozoic Geology of Central Oregon, by E. L. Packard. All but the first and last of these papers are illustrated with photographs of specimens found.

GENETICS

Chromosomes and Plant-Breeding. *By C. D. Darlington. The Macmillan Co., New York.* $1.75. $5\frac{1}{2} \times 8\frac{1}{2}$; xiv + 112; 1932.

Recent Advances in Plant Genetics. *By F. W. Sansome and J. Philp. P. Blakiston's Son and Co., Philadelphia.* $4.00 net. 5×8; x + 414; 1932.

These two books were written by members of the John Innes Horticultural Institution. Darlington's book is intended to indicate to horticulturists the service cytology may render in the practical conduct of breeding experiments. He points to a long list of cytological studies, some of them his own, on cultivated plants in support of his conclusion:

> While chromosome studies therefore do not give the plant-breeder any great control over his material, they enable him to direct his efforts into the right channels for obtaining and preserving the results likely to prove most profitable to him.

There is a good index and the bibliography is complete enough for an introductory text.

We could not entirely suppress the suspicion that a considerable part of the recent advances in plant genetics must have been made by reading the *Drosophila* literature. Certain it is that the mechanisms of inheritance in the fruit fly have been taken over bodily in very many instances to fill in gaps in the plant data. This being so, it is difficult for an American biologist to conceive "the unfortunate lack of contact that exists at present between the plant and animal branches of the science" which Sansome and Philp hope to remedy with their book. The principal development of the last ten years peculiar to plant genetics appears to be a growing appreciation of the importance of polyploidy as a factor in the heredity of crop plants. As in work on *Drosophila*, the widespread application of cytological methods has altered

the whole aspect of the science during the last decade and this book gives an account of developments during a period of extremely rapid growth. The book is well indexed and its bibliography runs to more than 1200 titles. It should be very useful to geneticists.

HEREDITY *in the Light of Esoteric Philosophy.* *By Irene B. Hudson.* *Rider and Co., London.* 3s. 6d. net. $4\frac{3}{4}$ x $7\frac{3}{8}$; 144; no date (1932?).

For some time it has been apparent that biology is on the way to higher and better things. We suspect that it will not be long until physics begins to sweat to maintain its place as premier purveyor of pseudo-scientific mysticism to the intelleboobectuals. [This is a portmanteau word composed by Reginald the Office Boy in the Classical Dodgsonian tradition. In reading aloud pronounce each syllable slowly and clearly and put the accent on the fourth syllable from the start.] The author of the present treatise, while plainly neither an Eddington nor a Millikan in intellectual stature, is, however, like the proverbial organist, doing her best. What she sets out to do is to reconcile, or better to unite theosophy and modern genetical theory. After a chapter composed of quotations from T. H. Morgan, Crew, R. R. Gates, and others, she gets to grips with her evolution and philosophy. The result is really swell stuff. Lack of space alone prevents us from doing it justice. It reeks with gems of thought like the following:

> The anthropoid apes are the "degenerate descendants" of this renewal and conscious sin. They are truly "speechless men," and are *millions of years later than the speaking human being.* They will become speaking animals (or men of a lower order) in a later cycle of evolution, while the Adepts of a certain school hope that some of the Egos of the apes of a higher intelligence will reappear at the close of the next Root Race.

VERERBUNGSLEHRE. *Mit besonderer Berücksichtigung der Abstammungslehre und des Menschen. Bd. I. Mendelismus. Zweite Auflage.* *By Ludwig Plate.* *Gustav Fischer, Jena.* 28 marks (cloth); 26 marks (paper). $6\frac{1}{4}$ x $9\frac{1}{8}$; x + 554; 1932.

The first edition of this *Vererbungslehre* appeared in 1913. Since that time the literature on genetics has increased to such an extent that in bringing the book up-to-date the distinguished author has found it necessary to publish the second edition in three volumes. This, the first volume of the expanded work, deals with the elements of cytogenetics, cleavage, multiple allelomorphism, multiple factors, and chromosome Mendelism (linkage, crossing-over, Morgan's theory, polyploidy and aberrant chromosomes). The second volume, on sexuality and general problems, is in press. Each volume has its own bibliography and index. There is still a third volume in preparation. This will consider the special genetics of the animals which have been most thoroughly studied, and the eugenics of healthy and sick persons. Plate is a wise, forthright, and occasionally salty writer, who may be read with profit if not always with complete agreement. This book when completed will have to be a part of the reference equipment of every biological laboratory.

PRINCIPLES OF GENETICS. *A Textbook, with Problems. Second Edition.* *By Edmund W. Sinnott and L. C. Dunn.* *McGraw-Hill Book Co., New York.* $3.50. $5\frac{7}{8}$ x 9; xvi + 441; 1932.

This second edition of a well and favorably known text-book on genetics represents a thorough revision of the old text and incorporates results of recent investigations which have led to important new ideas. More emphasis is laid on principles. The three chapters in the first edition devoted to applications of genetics in agriculture and human heredity have been omitted from this edition. Seduced by the prevailing Genetical Uplift the authors have added two new chapters on the application of genetics to biological theory. There is a more detailed consideration of the physical basis of inheritance. Many topics of importance omitted in the text itself are called to the attention

of the student in a series of Reference Problems at the end of each chapter. A list of references also follows each chapter. A discussion of biometric methods is appended, and there is a full index.

BUD VARIATION IN PEACHES. *U. S. Department of Agriculture Circular No. 212.*
By A. D. Shamel, C. S. Pomeroy and F. N. Harmon. U. S. Government Printing Office, Washington. 10 cents. 6 x $9\frac{1}{4}$; 21; 1932 (paper).
This circular is a report on a scientific study of bud variation in the trees of several important canning varieties of peaches which was begun in 1925 and has been continued to the present time.

These studies include annual individual-tree performance records in plots where the cultural and other conditions seem most favorable for this work. A systematic effort is being made to determine varietal characteristics by means of estimate-yield records, together with careful notes and illustrations of outstanding foliage and fruit characters.

Progeny tests of the variations are being made. Improved strains for commercial use will probably be developed from some of the variations that are described in this circular.

THE GENETICAL FACTOR IN ENDEMIC GOITER. *Carnegie Institution of Washington Publication No. 428. (Paper No. 37 of Department of Genetics.)*
By Charles B. Davenport. Carnegie Institution of Washington, D. C. 75 cents (paper); \$1.25 (cloth). $6\frac{3}{4}$ x 10; iv + 56 + 4 folding charts; 1932.
Endemic goiter is usually attributed to environmental conditions. But, since in an endemic region not everyone has goiter, and the goiter which is found tends to be in particular families, the hypothesis is advanced that the environment merely brings out a thyroid insufficiency based on gene defects which would go unnoticed if the conditions were entirely favorable. An investigation was made on families in a mountain valley in Western Maryland, the details of which are presented in this publication. In regard to the genetical factor, the conclusions are that two coöperating genes do the job: one sex-linked and dominant; the other autosomal and dominant.

MULE PRODUCTION. *U. S. Department of Agriculture Farmers' Bulletin No. 1341.*
By J. O. Williams. U. S. Government Printing Office, Washington. 5 cents. 6 x $9\frac{1}{2}$; 27; 1932 (paper).
An informative leaflet on the breeding and care of mules.

GENERAL BIOLOGY

EXPERIMENTAL ANALYSIS OF DEVELOPMENT.
By Bernhard Dürken. Translated by H. G. and A. M. Newth. W. W. Norton and Co., New York. \$4.75. $5\frac{5}{8}$ x $8\frac{3}{4}$; 288; 1932.
In this translation from the German, an excellent account is given of the present status and current major problems of analytical embryology. Following a consideration of methods of approach, the major problems are outlined as follows: 1. The determination of the *limits of potency* (of the uncleaved egg and its separate parts, of blastomeres, and organ rudiments) at different periods of development. By potency is meant the primary developmental capacity of the germinal region in the egg, which transcends the actual fate of the zygote. 2. *Regulative phenomena:* the production of a normal whole, following loss or change in one part of the developing organism. 3. *Determination of parts:* the narrowing down of the extensive potentialities of the germinal regions to what they will actually perform. 4. *Processes of realization* following determination processes: environment functions here as well as inherited factors. The problem arises as to whether environment has only individual, or also transindividual action. 5. Problems concerning the extent to which *interrelations* and *modifications* of the parts of the whole organism are functions of chemistry, energy-relations, etc. 6. Relative competence of the *genetic* and the *embryological approach* to deal with the problems of the internal factors in develop-

ment. 7. The importance of the *whole* organism in the process of development.

After this survey of the present fields of investigation, fertilization is considered. It is shown that the male and female reproductive cells are equivalent to one another, and that the essential in the process of fertilization is not the activation of the egg, but rather the union of two separate systems, very similar as regards their potency, to form a new individual. This union is not a mosaic-like apposition of two systems, but is the origin of a new unit and whole. This fusion reveals the presence of a specific organismic faculty which cannot be referred to any organization either mechanistically or morphologically explicable.

The remainder of the book is devoted to a discussion of the nature of development. Development is regarded as carried out by a special *reaction-basis*—the name given to the whole of the specific constitution of the germ cell, including those of its primary morphological differentiations which are essential to its development. The reaction-basis is the actual bearer of all the inherited internal factors of development. It does not contain a preformed particle of protoplasm corresponding to each single part of the resulting individual.

> It is more true to say that the egg—i.e. the individual in its unicellular condition—owes its general determination as regards purely specific and racial peculiarities to the reaction-basis, while determination of the morphological value of the separate parts follows step by step. The solution of the problem of the specific and racial determination of the whole organism would therefore involve an investigation of the real nature of the reaction-basis. Experimental embryology, as an analytical science, cannot, however, argue from the whole to its parts, but must arrive at a comprehension of the whole through understanding the parts. Hence . . . . the question of the determination of the parts is the essence of the determination problem. This determination comes about by degrees, earlier or later according to the kind of animal in question, so that an indeterminate condition gradually gives place to a determinate one. . . . . Not only does it lead little by little from the general to the particular, but the rigidly determined condition is connected by intermediate stages with the indeterminate condition, beginning with the first appearance of determination—when it is still indefinite—and proceeding to its final complete establishment.

In the final chapter, some of the difficulties which arise when the chromosome theory, with its rigid materialistic determinism, is considered in the light of the actual phenomena observed in experimental embryology, are discussed. It is concluded that

> . . . . the primary foundation of the reaction-basis is not a mosaic of discrete parts. It is the totality of the germ-cell, to which the individual constituents distinguishable in the cell are subordinated—whether these constituents can be passed on to the descendants more or less directly, or whether they must be reformed at the beginning of each new development, with the whole specific constitution of the reaction-basis as their starting-point. Development is Epigenesis.

EMIGRATION, MIGRATION AND NOMADISM. *By Walter Heape. Edited with a Preface by F. H. A. Marshall. W. Heffer and Sons, Cambridge.* 12s. 6d. net. $5\frac{1}{2} \times 8\frac{1}{2}$; xii + 369; 1932.

A book of deep interest to biologists. Its distinguished author did not live to see his book through the press, but that work has been ably done by F. H. A. Marshall, who also contributes a preface. In a lengthy introduction Heape outlines the growth of his ideas concerning the physiology of the reproductive system (which he believes to play a far more important part in the history of evolution than is generally recognized), the interrelations of the digestive and the reproductive systems, the cumulative effect of the gonadic secretions, the probable part played by vitamines on the growth and on the breeding excitant of animals, the causes leading up to the movements of animals from one territory to another, etc. The sections following the introduction are as follows: Territory; Emigration (three chapters); Diffusion, dispersal and drift emigration; Migration (two chapters); Hibernation and aestivation; Nomadism, and Conclusion.

The author defines the nature of the different kinds of voluntary movements of animals, drawing a sharp distinction between the terms emigration (permanent evacuation of home territory) and migration. He believes that

> "the conception of the possession of territory or of property is inherent in all animals capable of voluntary movement from place to place, that territorial rights are universally recognized and almost always strictly respected by all animals except 'raiders,' "

and that while territorial rights extend only over limited areas there are huge tracts of neighboring country which are clearly recognized, except by predaceous animals, as neutral territory. Incentives to individual movement are classed as alimental, climatic, and gametic. These arise from quite different physiological influences. The combined effects of excessive reproduction over a definite tribal area and the consequent scarcity of food which leads to mass movements are extensively discussed. The source of the impulse to migrate for breeding purposes he suggests is derived from "the same gonadic secretion, which I called 'gonadin,' that is responsible for the growth of the secondary sexual characters, which also precedes sexual activity."

He is inclined to believe that

> "the origin of what I have called an epidemic of hysteria will also be found to be associated with some pathological change in an organ of the reproductive system. The simultaneous exhibition of this hysterical condition in all the members of a large number of herds occupying a definite territorial area is a very remarkable incident. I imagine it may primarily be due to a change in the quality of the food supply of that area; and I hazard the suggestion that the normal functional activity of the gonads is thereby interfered with, either unduly excited or checked."

The frequent selection of unfavorable routes by mammals undergoing mass emigration which ultimately lead to death, is possibly due to the fact that they choose the only route available if the rights of territory of others are to be respected. The author gives in the final chapter a brief note on Evans' and Burr's work (1925). The work concludes with a lengthy bibliography and an index.

Problems of Relative Growth.

By Julian S. Huxley. The Dial Press, New York. $3.50. $5\frac{1}{2}$ x $8\frac{3}{8}$; xix + 276; 1932.

This book is a useful review of the literature on the differential growth of the parts of organisms and related topics. It is very fully and well illustrated, documented, and indexed. On these accounts it will be of service to all students of the problems of growth. In respect of the ideas which it embodies the book owes a very great deal to D'Arcy Wentworth Thompson, to whom it is appropriately dedicated. The material is organized and presented with great skill. The general conclusions reached are:

> Starting from the fact of obviously "dysharmonic" or heterogonic growth, we have discovered our first new empirical law—the law of constant differential growth-ratio. We have then recognized that it is only a special case of the law of differential growth-partition, which is the prime quantitative basis of relative growth. Passing on from that, we have found a further and quite unexpected empirical law—that the existence of a differential growth-ratio in an organ or region seems always to be associated with a growth-gradient culminating in a growth-centre; or in other words, that the distribution of growth-potential is not marked by discontinuities or by frequent oscillations, but occurs in an orderly and continuously graded way. And we then showed that these localized growth-gradients were but special cases of growth-gradients permeating the whole body. These laws, however, only appear to apply to the stages of growth occurring after histological differentiation has been completed. Very rapid growth, obeying quite other laws, occurs during the earlier period. For these two phases of development, the terms histo-differentiation and auxano-differentiation are proposed.

Riddles of Science.

By Sir J. Arthur Thomson. Liveright, New York. $3.50. $5\frac{3}{4}$ x $8\frac{5}{8}$; 387; 1932.

Although this is written for the layman the author covers a wide range of subjects, with lucidity and an admirable scientific caution. Any chapter, picked at random, proves a complete and entertaining whole. The subjects are for the most part presented in the form of a question, an effective manner to catch the attention of the general reader. The first part deals roughly with general physiological riddles ranging from such different questions as "How does life begin?," "Why must we die?," to "What are hormones?," "Why do we laugh or cry?," "Why does your hair turn grey?," etc.

Part II deals with problems of natural history, such as "Riddles of the country side," insects, galls, the homing instinct, and "Natural wireless" which leads directly into the third part in which the author attacks psychological phenomena. We cannot but respect his unprejudiced treatment of telepathy, clairvoyance and

crystal gazing. In Part IV the author discusses Evolution, and what is behind it all. There is a charming epilogue on the "Wonders of the world."

The book is highly to be recommended as a thoughtful, intelligent and conservative explanation of many of the questions which occur to the inquiring mind. There is no index.

Movement and Localization of the Presumptive Epidermis in Triturus Torosus (Rathke). *University of California Publications in Zoology, Vol. 36, No. 13.*
By A. Mandel Schechtman. University of California Press, Berkeley. 25 cents. $7\frac{1}{8}$ x $10\frac{3}{4}$; 22 + 6 plates; 1932 (paper).

This contribution to the study of developmental mechanics in the amphibia is based on the application of the Vogt method of vital staining to embryos of *Triturus torosus*, the common newt of the Pacific Coast. Stains are made on different localities of embryos of different stages, and their fate followed as the embryo develops. Among the results, which are presented in summary, are the following:

> Marks made on the germinal area (*Richtungsfleck*) appear on or adjacent to the anterior margin of the medullary plate. Presumptive epidermis and medullary materials are contiguous in the region of the animal pole as early as the zygote stage. Presumptive epidermis occupies approximately the ventral half of the embryo in the slit-shaped blastopore stage; presumptive medullary material occupies the remaining dorsal half.

The progress of the presumptive epidermis of tail, caudal fins, head, mandibular arch and brachial area is also indicated.

Recent Advances in Cytology.
By C. D. Darlington. P. Blakiston's Son and Co., Philadelphia. $4.00. $5\frac{1}{8}$ x $7\frac{7}{8}$; xviii + 559; 1932.

In the preface the author states that the

> present work attempts to describe one aspect of cytology, the study of the nucleus and the chromosomes in plants and animals. It consists of three elements: an introduction for the student who is a beginner, a résumé for the research worker who requires classified observations, and a theoretical treatise, in which my own views are developed, for the general biologist.

Students and investigators will find this a useful book. The work has been done conscientiously. Many will disagree with the author's interpretation of previous morphological studies of nucleus and chromosomes and attack his theories as unsound or obscure. Nevertheless his views are entitled to consideration, particularly by the research worker and the general biologist, who cannot fail to find many of his hypotheses conducive to new points of view. The book is well documented and illustrated. In a group of four appendices he discusses cytological interpretations, and recent improvements in technique, and gives a glossary and lengthy bibliography. J. B. S. Haldane contributes a foreword. There is a subject index.

Nonsuch: *Land of Water.*
By William Beebe. Brewer, Warren and Putnam, New York. $3.50. $5\frac{7}{8}$ x $8\frac{5}{8}$; xv + 259; 1932.

In this group of essays Doctor Beebe tells with his usual charm of the animal and plant life, marine and terrestrial, of Bermuda. We follow him in his underwater adventures on the shoals and reefs; we watch the behavior of the peacock flounder with its periscope eyes and the birth of the young seahorses from the pouch in which their father has incubated them. Other interesting essays deal with the cedars and how they came to Bermuda, with the migration of birds and lemmings and eels, with sharks and crabs and snails. This is the first of a series, one of which is to describe the author's observations on the life of the deep sea, while others will be devoted to the life histories of Bermuda fish. There is an index.

Biology. *An Introduction to the Study of Life.*
By H. Munro Fox. The Macmillan Co., New York. $1.75. $4\frac{3}{4}$ x $7\frac{1}{4}$; xv + 344; 1932.

This little book is designed primarily for elementary and high school teaching, hence the presentation is simple with a

minimum of technical detail. The author adopts the method of teaching whereby one begins with man and ends up with fossils. We question the advisability, however, of introducing a student immediately to physiological problems of respiration, digestion and circulation; further, it is questionable if he gets a very clear conception of the actual evolutionary sequence from simple forms to complex ones. Apart from this criticism, there is much to recommend this book; the author appreciates the value of stimulating a naturalistic feeling for biology, and gives many suggestions for simple and interesting experiments that any young student can perform by himself.

ELEMENTS OF BIOLOGY.

By C. von Wyss. With a Foreword by Sir J. Arthur Thomson. Christophers, London. 6 shillings net. 5 x 7⅝; xvi + 326; 1932.

We take pleasure in recommending this charming and accurate introduction to the study of biology. Although this book was written primarily for children, adults who wish to familiarize themselves with this subject will find it interesting and stimulating. Miss von Wyss begins the book with the march of the seasons; then goes on to the process of living, the fitness and progress in living, and the relation of organisms to their environments; and ends it with a chapter citing instances in which man's knowledge of the biology of plants and animals has aided in his welfare.

A SURVEY COURSE IN GENERAL BIOLOGY.

By James G. Needham. Comstock Publishing Co., Ithaca, N. Y. $2.70. 5¼ x 7½; vii + 376; 1932.

The book is planned for those who are not specializing in biology, hence controversial matters, recondite theories, and discussions of animals with which the student may not easily familiarize himself are omitted. The author sticks to the conventional pedagogic order of exposition; that is, from the simpler forms to the complex. In this way he succeeds in emphasizing the logic of the science of biology, which it seems, at present, to be the fashion to ignore in biological teaching. An excellent text, highly recommended.

FUNDAMENTALS OF BIOLOGY. *Second Edition.*

By Arthur W. Haupt. McGraw-Hill Book Co., New York. $3.00. 5¾ x 9; x + 403; 1932.

The second edition of this useful textbook follows the same conservative presentation of material as the first (reviewed here in Volume IV, pp. 265–266). Emphasis is laid rather on cultural aspects than technicalities, as the book is designed for elementary courses. Nevertheless the fundamental facts of both botany and zoology are soundly and interestingly presented.

HUMAN BIOLOGY

CASTE AND RACE IN INDIA.

By G. S. Ghurye. Alfred A. Knopf, New York. $4.00. 6 x 9¼; vii + 209; 1932.

This book, written by an Indian of high scholarly attainments, will find a wide circle of interested readers. The author shows that there is nothing mysterious or sacred in the institution of caste. It is simply a highly exaggerated variation of the social differentiation which has existed from time immemorial amongst groups of societies throughout the world. The rigidity of this particular system is due to the fact that caste membership depends upon birth and that each group is governed by its own minute rules as to religious and social customs, diet, etc. There is a definite scheme of social procedure among the castes, the Brahmin standing at the head of the hierarchy and the untouchables falling into the very lowest group, with numerous classes and subclasses in between the two. Mr. Ghurye has nothing to say in favor of the present caste system. Neither does he see a favorable solution of the problem in the near future. He shows in a general survey of caste development from earliest historical to modern times how the present extremely complicated and evil situation has

naturally developed, and discusses the various methods which have been proposed to either abolish or modify its strangling hold on Indian peoples. He believes it the duty of every educated and progressive Hindu leader to ignore caste. Possibly the greatest blow to it will come from the educated young men and women of India who insist upon freedom in marriage.

Anthropologists will be interested in his section on Race and Caste in which he analyzes and compares bodily measurements made on racial and caste groups of Indians. In an appendix he gives these measurements in tabular form. The volume is well documented and indexed.

THE CHANGING CULTURE OF AN INDIAN TRIBE.

By Margaret Mead. Columbia University Press, New York. $4.50. $5\frac{7}{8}$ x 9; xiv + 313; 1932.

Scientific investigations of the American Indians have heretofore been confined mostly to a recording of what their aboriginal cultures were before and during the early period of their contact with that of the white man, and what has happened to them since has been neglected by the student of culture history. Dr. Mead spent four months on a reservation in the Mississippi Valley, and in this book gives an account of the disintegration and partial reintegration of the tribe which she here calls Antler. She pays particular attention to the Indian woman in transition, and this book may be considered as a contribution to the study of woman in general.

Little remains of the Antler's former culture. However, he has not as yet been very successful in adjusting himself to that of white society, especially its economic behavior. This is particularly true of the man.

> The social elaborations of gens, chieftainship, society, war police, have vanished, to leave only the household and the social dancing lodge; it is the women who are now the core of Antler culture. It is the women who are able to teach their daughters the dancing steps, the household arts, which are all that are left of the culture. The men are Indian by virtue of blood, language, and a disinclination to accept the economic behavior and economic attitudes of white society. But the women are still Indian in positive terms, in a multitude of details which bind mother to daughter and both to the grandmother.

An appendix contains tabular and diagrammatic treatment of raw materials, including household organization, marital situation, case histories of delinquent girls and women, and sample conversations. The book has an index but no bibliography.

A PRELIMINARY STUDY OF THE RUINS OF COBÁ. QUINTANA ROO, MEXICO. *Carnegie Institution of Washington Publication No. 424.*

By J. Eric Thompson, Harry E. D. Pollock and Jean Charlot. Carnegie Institution of Washington, D. C. $4.50 (paper); $5.50 (cloth). 9 x 12; vi + 213 + 12 plates + 6 folding charts; 1932.

Cobá, one of the largest of the known Maya cities, is situated in Mexico close to the Yucatan border in a region far more favorable to colonization than is usually to be found in the interior of the Yucatan Peninsula. A series of small lakes furnishing a permanent water supply, an abundant rainfall, and an almost tropical vegetation, undoubtedly made this a highly desirable habitat for the Mayas. The date of the destruction of the city is unknown, although some brief historical notes possibly indicate that it was around 1212 A.D. Since 1926 several expeditions have been sent out by the Carnegie Institution to Cobá and the vicinity. In this volume are recorded the results of these studies. The *Introduction* is by J. Eric Thompson. Harry E. D. Pollock contributes the next two sections on *Description of the Ruins* and *Architecture*. The fourth section is by Mr. Thompson on the *Monuments of the Cobá Region*, and this is followed by *Art Analysis of the Macanxoc Stelæ*, by Jean Charlot. In the final chapter Mr. Thompson discusses what conclusion can be drawn at present concerning the importance of Cobá as a cultural center and its influence and relations with other cities to the eastward and in Northwest Yucatan. He points out that in the past "too many outlines of Maya history have been built up on a very slender basis"

and that only when extensive studies of Maya ceramics and architectural developments have been made can Maya history be reconstructed. Excavations when undertaken at Cobá may possibly furnish many clues now missing.

The volume is issued in the usual very excellent format of these publications and contains excellent maps and reconstruction diagrams, also numerous very fine photographic reproductions. It is well documented and indexed.

Employment of Mentally Deficient Boys and Girls. *United States Department of Labor, Children's Bureau Publication No. 210.*

By Alice Channing. U. S. Government Printing Office, Washington. 15 cents. $5\frac{7}{8} \times 9\frac{1}{8}$; v + 107; 1932 (paper).

This is the report of a study made to determine the industrial adjustment of mentally deficient boys and girls after they leave the special classes in the public schools or the public institutions for the feeble-minded. Part I deals with former special-class pupils in Newark, Rochester (New York), Detroit, Cincinnati, Los Angeles, San Francisco and Oakland. As a rule, the I.Q. of these pupils was below 75. The interval between the date they had left the school and the date they were interviewed ranged from three to seven years. In all, 1,067 former pupils were investigated. The group studied is discussed with regard to sex, economic condition of families, I.Q.'s, physical defects, school progress and delinquency records. The information in each case is summarized in tabular form. Entrance upon working life is then considered, and the continuity of employment, occupations undertaken, wages received and success in jobs. The various topics are illustrated with case-history material. The results of the whole study are summarized and conclusions drawn. The need for the development of a system of placement and supervision for pupils from special classes is indicated.

Part II presents a similar study made on boys and girls formerly in Illinois State Institutions for the Feebleminded. The indications are that boys from the institutions did not have as favorable work experiences as those from the special classes. A much larger number had serious court records for delinquency. This fact points to the great need for follow-up work for those leaving the institutions.

Criminology.

By Robert H. Gault. D. C. Heath and Co., Boston. \$3.48. $5\frac{7}{8} \times 8\frac{3}{4}$; ix + 461; 1932.

Gault puts great emphasis on the psychological and pathological approach to the study of criminology. He believes that the greatest sources of our behavior are acquired attitudes which develop out of infinitely numerous reactions to our environment, these reactions depending upon native capacity, prepotent reflexes, and other influences. Numerous case histories, particularly those of the young, are given and the development of criminal attitudes is traced as they arise through unfortunate home influences, evil companionship, or other adverse social contacts. The book is divided into two sections. Under the heading *The criminal personality* we find such subjects discussed as personality, emotion, intelligence of criminals, psychopathic personality, epilepsy, race and sex, attitudes, from the gang to organized crime, and heredity in relation to criminality. The second part, *The struggle against crime*, deals with institutional and extra-institutional treatment of criminals, methods of obtaining evidence, and preventing the development of criminals. In a series of three appendices are discussed training courses for prison and police officers, programs of criminologic research institutes, and a plan for a crime prevention bureau. The book contains a number of tables, literature lists at the conclusion of each chapter, and an index. Jerome Davis has written an introduction.

Prospecting for Heaven. *Some Conversations About Science and the Good Life.*

By Edwin R. Embree. The Viking Press, New York. \$1.75. $5 \times 8\frac{1}{8}$; 185; 1932.

The physical sciences have given us a control over our environment much greater

than our forefathers possessed, yet we are still far from satisfied with our own lives. In this symposium the author gives his version of what may be expected of the mental sciences towards a happier and more satisfying life. C. M. Hincks, Medical Director of the United States and Canadian National Committees for Mental Hygiene, tells what is being done for the cure of the insane and the adjustment of the feeble-minded to their environment; Victor G. Heiser, Director for the Far East of the health work of the Rockefeller Foundation, describes the achievements of medical science; Franz Alexander, the distinguished psychoanalyst, presents the contribution of his subject towards sane living; Charles H. Judd, Director of the School of Education of the University of Chicago, tells of the rôle of education in preparing the individual for life; and Howard W. Odum, Director of the Institute for Research in Social Science of the University of North Carolina, describes the contribution which sociology may make towards a more satisfying social order. While the conversations did not take place in precisely the form recorded in the book, the members of the symposium accept them "as conveying accurately some at least of our ideas as to possible scientific steps to the good life." There is no bibliography or index.

THE TRIAL OF JEANNE D'ARC. *Translated into English from the Original Latin and French Documents, by W. P. Barrett. With an Essay* On the Trial of Jeanne d'Arc *and* Dramatis Personae, *Biographical Sketches of the Trial Judges and other Persons Involved in the Maid's Career, Trial and Death, by Pierre Champion. Translated from the French by Coley Taylor and Ruth H. Kerr.*

Gotham House, New York. $4.00. $6\frac{1}{4}$ x $9\frac{1}{4}$; xiii + 544; 1932.

This is the first complete translation into English of the official record of the trial of Jeanne d'Arc. The historian and the student of mystic phenomena and of witchcraft will find in it valuable material, while the general reader cannot but admire the fortitude of the peasant girl of nineteen, without counsel, and pitted against so many subtle theologians. Champion in his discussion of the trial agrees with Anatole France as to the partiality of the judges, and emphasizes the great share which the University of Paris, then the chief theological authority of the church, had in urging on the prosecution. In reading the trial record one cannot but wonder at the subsequent canonization of Jeanne. Her constant appeal is from the Church Militant to God. In short, Shaw's interpretation of her as the first Protestant seems to have much in its favor. The book has a bibliography of four pages, but no index.

MISCHIEFS OF THE MARRIAGE LAW. *An Essay in Reform.*

By J. F. Worsley-Boden. Williams and Norgate, London. 21 shillings net. $5\frac{1}{2}$ x $8\frac{1}{2}$; 427; 1932.

This is a somewhat dull, but extremely sound and solid legal treatise on the evolution, anatomy, and pathology of English marriage laws, civil and canon. Patiently, thoroughly and unemotionally the author lays bare in a devastating manner the absurdities of the English attitudes, as congealed into law, regarding marriage and divorce. He is, to be sure, *au fond*, a reformer and uplifter. He wants something done about it. But if all uplifters were as scholarly, patient, temperate, and fair as Dr. Worsley-Boden their critics would be largely disarmed. The essence of the reform advocated is simple and reasonable. It involves

> a definite rejection of the ecclesiastical view, as that view has been inherited from the long reign of the Papal canon law. It attributes the failure and unreality of the present law of England to the undue influence of the canon law in principle and practice; and, incidentally, it carries the contention that the ecclesiastical view, as expressed in the indissolubility of marriage, is not the best expression of the Christian religion.

BUT FOR THE GRACE OF GOD.

By J. W. N. Sullivan. Alfred A. Knopf, New York. $2.50 net. 5 x $7\frac{1}{2}$; 220; 1932.

This entertaining book constitutes, among other things, a case history worthy of careful study by the human biologist. J. W. N. Sullivan, whose autobiography it is,

is a remarkable man. With a thorough, profound, and wide-ranging knowledge of mathematics and physics, and quite unable to be happy if long away from the atmosphere of the research laboratory, his outstanding achievement has been as a popularizer of the most recondite fields of mathematical physics. With all the essential equipment in the way of innate ability and technical knowledge far beyond that of many an F.R.S. he has never been a productive researcher. The reason, in his own words, is: "I had no creative ability, either as a writer or as a man of science."

The book is equally revealing about practically every other aspect of the author's life. This is what makes it so superb a case record. His amorous adventures, his passion for music which had as one result the writing of one of the best books on Beethoven ever produced, his spiritual restlessness, are all exposed and searchingly analyzed. This is a book which every young biologist starting his career should read. It lacks an index.

Roman Britain. *The Objects of Trade.*
By Louis C. West. Basil Blackwell, Oxford. 5 shillings net. $5\frac{1}{4} \times 8\frac{1}{2}$; iii + 108; 1932.

This little book contains in summary form a complete account, so far as the records show, of articles of trade and industry of Roman Britain covering the period between the time of Claudius and the fourth century. In each section the author discusses briefly the types of objects and their use and then in tabular form lists the object, its source, where found and authority. The objects exported range from forest products and cultivated plants through sea foods, pottery and metals to building stone. It will surprise many to learn that the British Isles produced precious and semiprecious stones. From the river mussels came pearls which, although of no very great value, apparently were much desired by the Romans. Pottery was imported in great quantities as were also wine, oil, bronzes and glassware. The author includes a list of British and foreign traders of the same period.

Digressions of a Man of Science.
By Sir A. Daniel Hall. Martin Hopkinson, London. 7s. 6d. net. $5\frac{1}{2} \times 7\frac{3}{4}$; 223; 1932.

In reading *Digressions of a Man of Science* we can easily imagine ourselves seated in a comfortable chair listening to Sir Daniel Hall speak in a pleasant, roaming fashion of his ideas and interests. These range from a scientific attitude towards faith to the culture of tulips. His primary interest, though, is in the research field of agriculture, its value and again its inconsistencies. He says that "the state must have research in order to obtain efficiency, but does mankind really care about efficiency?" Our author answers negatively and says man only wants to "loaf and possess his soul." This attitude is carried out in the book as the writer's various mental hobbies are treated with easy but pleasant lack of continuity. Writing is his digression and reading he would like to make yours.

The Causes of War. *Economic, Industrial, Racial, Religious, Scientific and Political.*
By Sir Arthur Salter, Sir J. Arthur Thomson, G. A. Johnston, Alfred Zimmern, C. F. Andrews, Frederick J. Libby, Henry A. Atkinson, Wickham Steed and Others, as Rapporteurs of the Various Sections of Commission I. of the World Conference for International Peace Through Religion—as Submitted to the Executive Committee for Presentation to the World Conference. With Introduction by Ruth Cranston. Edited by Arthur Porritt. The Macmillan Co., New York. \$1.50. $5\frac{1}{2} \times 7\frac{3}{4}$; xxix + 235; 1932.

This report is confined to an exposition of the causes of war and the tendencies that make for war. Probably no great war in the past has been due to a single cause, and the most apparent has not always been the most fundamental. Political and economic factors, which are now the most important factors leading to war, are especially intertwined. Concerning future wars we quote from Mr. Steed:

> The feeling of insecurity, and the fears which it engenders, are undoubtedly the strongest potential causes of war in the world to-day. No nation,

whether it belong to the League or not, and no signatory of the Paris Peace Pact, can be certain that, if it reduces its armaments to a point at which it would have to rely upon the help of others for defence against attack, such help would really be forthcoming.

On the Aboriginal Inhabitants of the Andaman Islands.

By Edward H. Man. With Report of Researches into the Language of the South Andaman Island, by E. J. Ellis. Royal Anthropological Institute, London. 8s. 6d. + 6d. for postage. $5\frac{3}{4}$ x $8\frac{3}{4}$; xxxii + 254; 1932.

This is a welcome reprint of one of the classics of anthropology and ethnology, for a long time not readily accessible in its original form. Edward H. Man was Assistant Superintendent of the Andaman and Nicobar Islands, and resided among the aboriginal inhabitants from 1869 to 1880. His account of them was originally published in 1885 in the *Journal of the Anthropological Institute of Great Britain and Ireland.* It is a fine piece of work, systematically touching upon every aspect of the native lives, customs, habits, somatology, physiology, etc. The author's keen powers of observation were supplemented by a sympathetic insight into native ways of thought, and tolerance of differences of outlook and habit rare among officials, even to this day. Altogether it is a great service to anthropology to make this work available in separate form. It is well documented and indexed.

The Lame, the Halt, and the Blind. *The Vital Rôle of Medicine in the History of Civilization.*

By Howard W. Haggard. William Heinemann, London; Harper and Bros., New York. 21 shillings net (England); $4.00 (U. S. A.). 6 x 9; xxiv + 420; 1932.

The subject of this book is the influence of medicine on civilization.

> Medical history is world history. Some phase of medicine has been involved in every great historical event, but usually these medical aspects have been ignored or overlooked. Consequently, when you turn to them they take you away from the beaten path of history and lead you instead into little-known byways of history. Yet, for everyone, medical history is probably more important than any other phase of history, for medical history discloses the forces that have made our modern civilization possible.

The thesis is developed through narrative, copious anecdotes, and delightful illustrations. The book is a worthy successor to the author's now famous *Devils, Drugs and Doctors.*

Fundamental Administrative Measures in Physical Education.

By Frederick R. Rogers. The Pleiades Co., Newton, Mass. $2.75 net. 6 x 9; xvi + 261; 1932.

Decidedly one of the most sensible treatments of the subject that has appeared since physical education has attained academic recognition. The author has reviewed the field thoroughly and presents in addition a lucid philosophical discussion of the value of anthropometric measurements. We like his attitude towards physical education as expressed in the following:

> Joy is a great immediate health tonic. It is even possible that the total effects of health and vitality of a game of checkers played with intense enjoyment will be more beneficial than a basketball battle "played" under protest in a spirit of rebellion and hate.

Man Comes of Age.

By John Langdon-Davies. Harper and Bros., New York. $3.50. 6 x $9\frac{3}{8}$; x + 265; 1932.

As usual, our author has a great many words to say but perhaps it takes a good many to tell us what science has done to our philosophy and attitude towards daily life; and what science does or will do to settle the perplexities of existence. He tends only to present the problem, which of course has been done many times. Science can account for matter but not altogether for human behavior, for he admits we are of a "naughty world."

Wild Oats.

By Eric Muspratt. Gerald Duckworth and Co., London. 8s. 6d. net. $5\frac{1}{2}$ x $8\frac{1}{2}$; 237; 1932.

This extraordinary book, written in the most approved realistic manner, with all the shocking words spelled out in full, tells the story of the author's adventures and his thoughts about them in bumming his way from England through France, Italy, Austria, Hungary, Germany, and Holland, and back to England. "Bumming" is the correct word. Mr. Muspratt plainly likes the life of a hobo, and perhaps likes still better to tell about it. He writes with considerable skill, and is robustly pleased with himself. The result is a significant social document which is also an entertaining book.

Welfare of Children of Maintenance-of-way Employees. *U. S. Department of Labor, Children's Bureau Publication No. 211.*
By Helen R. Wright. U. S. Government Printing Office, Washington. 15 cents. $5\frac{3}{4}$ x $9\frac{1}{4}$; v + 192; 1932 (paper).
A report of a field study, carried out in different parts of the United States, on the income, expenditures and living conditions of families of section-workers on the railroads. 550 families with 1,674 children comprise the group studied. The field work was completed in 1929, before lower wages, part-time employment or no employment reduced the family income, but even so the report presents a picture of insufficiency.

Juvenile-Court Statistics, 1930. *Based on Information Supplied by 92 Courts. Fourth Annual Report. United States Department of Labor, Children's Bureau Publication No. 212.*
U. S. Government Printing Office, Washington. 10 cents. 6 x 9; iii + 69; 1932 (paper).
This report consists of three parts: I. General discussion and summary tables; II. Comparative delinquency rates for 1930 and the 3-year period 1927–1929; III. Source tables. In courts having jurisdiction over children up to 18 years of age, 16 and 17 year old children were most frequently delinquent. Stealing and acts of carelessness or mischief were the most usual offenses of boys, whereas running away, being ungovernable, and sex offenses were most common among girls.

The Races of Man. *Differentiation and Dispersal of Man. Physical Anthropology.*
By Robert B. Bean. The University Society, N. Y. 6 x 9; vi + 134; 1932 (paper).
This little book traces some of the steps in man's ascent and the evolution of special attributes, points out the main routes of race dispersal and describes briefly the characteristics of the chief races and their subdivisions. There are suggestions for further reading, a glossary and an index.

The Social Selection of Human Fertility. *The Herbert Spencer Lecture Delivered at Oxford 8 June 1932.*
By R. A. Fisher. Oxford University Press, New York. 70 cents. $4\frac{1}{4}$ x $6\frac{7}{8}$; 32; 1932 (paper).
In this lecture Fisher again argues in favor of a system of family allowances to counterbalance the effect of the social promotion of the less fertile and the consequent association of ability with infertility.

ZOÖLOGY

A Naturalist in the Guiana Forest.
By R. W. G. Hingston. Longmans, Green and Co., New York. $5.00. $5\frac{1}{2}$ x $8\frac{1}{2}$; xiii + 384; 1932.
This book is primarily an account of a novel and unique bit of zoölogical exploration, namely the study of the fauna of the tree-tops of a tropical forest. British Guiana was the *locale*, and the expedition directed by the author, Major Hingston, the distinguished English entomologist, went out under the auspices of the Oxford University Exploration Club.

The problem was to establish observation posts in the tree-tops and collect and study from them the inhabitants of the forest canopy. This was no easy matter. The average height of the roof was about 100 feet. Climbing that big a tree, under the conditions imposed by a tropical for-

est, is not done without taking thought. The expedition took out all sorts of gear from home, much of which proved in the end to be useless in practice. The native Indians really turned the trick for them; carrying up ropes with the help of climbing irons, and taking the first steps to rig blocks and tackles with which observation chairs could be run up and down.

As a piece of pioneering the work was a great success.

> We were fairly satisfied with these rough efforts to study the animal life of the canopy. Apart from observations on the habits of the species—which constituted our main objective—we secured from the roof specimens of about 2,000 animals and 4,000 sets of plants. We fully realized, however, the primitiveness of our methods. The job was being done for the first time, and when leaving England we had only vague ideas of the way in which it ought to be tackled. We just brought along a heap of miscellaneous gear and made use of the contrivances that turned out most serviceable. That is the way of learning the first steps in an operation, and the experience gained has naturally exposed its rudimentary character and many imperfections.

The book is divided into two parts, both beautifully and effectively illustrated. The first part gives a running narrative of the expedition and a superb brief description of the general biology of a tropical forest. The trees make up

> a selfish mob of ruthless competitors, every individual elbowing its companion out of the way, seizing and clinging to the least opportunity, until in the end a few of the most favoured ones pushed themselves as conquerors through chinks in the canopy. . . . The whole spectacle of forest within forest was a wonderful example of riotous struggle.

The second part is a series of essays on the natural history of various forms of life encountered, particularly spiders and insects.

Altogether it is a notable contribution to current biological literature. We recommend it warmly to our readers. It has a good index.

AN INTRODUCTION TO ZOÖLOGY *Through the Study of the Vertebrates with Special Reference to the Rat and Man.*

By Zeno P. Metcalf. Charles C. Thomas, Springfield, Ill. \$3.50. $6\frac{1}{8}$ x $9\frac{1}{4}$; xix + 425; 1932.

This textbook departs from the more customary methods of introducing zoölogy to college freshmen. Instead of presenting a series of animal types starting with protozoa and ending with man, the author chooses one vertebrate, the rat, to be studied in detail so that the student may see how structure and functions are related. The book divides into three parts: (1) A general introduction, concerned with a summary of the various branches of zoölogy, and a brief classification of the animal kingdom; (2) the detailed study of the morphology and physiology of the rat, with comparisons from other groups of vertebrates; and (3) the broader aspects of biology (eugenics, sociology, psychology and agriculture). No doubt this method of teaching will have an appeal to the average student of zoölogy who is chiefly interested in why he operates as he does; but it is open to question whether the invertebrates are not pedagogically important enough to merit at least a few weeks of attention in an elementary college course.

A PRELIMINARY STUDY OF THE NITROGEN NEEDS OF GROWING TERMOPSIS. *University of California Publications in Zoölogy, Vol. 36, No. 15.*

By Elizabeth S. Roessler. University of California Press, Berkeley. 25 cents. $7\frac{1}{8}$ x $10\frac{3}{4}$; 12; 1932 (paper).

Some investigators have found that termites are able to live on a diet solely of filter paper and water with no other elements present that are generally considered necessary for life; they have even gone so far as to assert that termites can grow just as normally on pure cellulose as on a diet of wood. Miss Roessler, using more care in experimental technique, found that termites fed on a diet of filter paper, although they did grow, did not do so as rapidly nor as well as those fed on wood. Another interesting result to come out of this study is the fact that instars fed on a filter paper diet do not develop normal wing pads. The author makes the suggestion that

> the development of first forms, and hence of other castes, is conditioned by the diet; but the development of wing pads is not necessarily caste development, therefore any general conclusions in this regard would be untimely.

THE FOOD OF PROTOZOA. *A Reference Book for Use in Studies of the Physiology, Ecology and Behaviour of the Protozoa. The Egyptian University Publications of the Faculty of Science No. 1.*

By H. Sandon. Misr-Sokkar Press, Cairo. Piastres 20. $6\frac{3}{4} \times 9\frac{1}{2}$; ii + 187; 1932 (paper).

This book is the outgrowth of a study on the biological relationships of the protozoa of soil and of sewage disposal works which the author made while at the Rothamstead Experimental Station in England. It is a useful review of present day knowledge of what protozoa feed on, involving the consideration of many questions concerning the physiology and behavior of these forms Among these ancillary topics are the digestive mechanism of protozoa, symbiosis, quantities of food consumed by different forms, requirements of the organism for growth and activity, morphology of the feeding mechanism and stimuli to which the organism can react. In presenting the material the author treats each organism systematically according to order and family. A bibliography of 447 titles is given and author and subject indices.

METHODS FOR THE IMPROVEMENT OF MICHIGAN TROUT STREAMS. *Bulletin of the Institute for Fisheries Research No. 1.*

By Carl L. Hubbs, John R. Greeley and Clarence M. Tarzwell. Institute for Fisheries Research, University of Michigan, Ann Arbor. 50 cents. 6 x 9; 54; 1932 (paper).

This bulletin is a comprehensive survey of problems and questions associated with stream improvement. The practicability of such a project is considered. The planning and carrying out of the work, and the most satisfactory techniques available (dams, deflectors, and covers) are described. A list is given of the materials and equipment needed.

ON TOKOPHRYA LEMNARUM STEIN (SUCTORIA) WITH AN ACCOUNT OF ITS BUDDING AND CONJUGATION. *University of California Publications in Zoölogy, Vol. 37, No. 16.*

By Alden E. Noble. University of California Press, Berkeley. 50 cents. 7 x $10\frac{3}{4}$; 44 + 6 plates; 1932 (paper).

This is principally a cytological study of the life history of *Tokophrya lemnarum* with particular reference to its micronucleus. The internal budding of this protozoon is of interest. Although it was found on the roots of other aquatic plants in abundance, curiously enough *T. lemnarum* was never found on *Lemna gibba*.

THE BED-BUG: *Its Habits and Life-History and How to Deal with It. British Museum (Natural History) Economic Series No. 5. Third Edition, Revised, Enlarged, and Partly Rewritten by Major E. E. Austen.*

By Bruce F. Cummings. British Museum, London. 2d. $5\frac{1}{2} \times 8\frac{1}{2}$; 27; 1932 (paper).

A third revised edition of this useful little pamphlet (originally published fifteen years ago) on these troublesome insects and how to get rid of them.

PUBLICATIONS OF THE UNIVERSITY OF OKLAHOMA BIOLOGICAL SURVEY. *Volume IV, No. 1. Oklahoma Spiders, by Nathan Banks, N. M. Newport and R. D. Bird. No. 2. Dragonflies of Oklahoma, by R. D. Bird.*

University of Oklahoma Press, Norman. 60 cents. 6 x 9; 57; 1932 (paper).

This bulletin contains lists of spiders and dragonflies collected in Oklahoma and notes on common Oklahoma spiders.

AMPHIBIANS AND REPTILES FROM LOWER CALIFORNIA. *University of California Publications in Zoölogy, Vol. 38, No. 6.*

By Jean M. Linsdale. University of California Press, Berkeley. 35 cents. 7 x $10\frac{3}{4}$; 42; 1932 (paper).

DESCRIPTIONS OF NEW BIRDS FROM OREGON, CHIEFLY FROM THE WARNER VALLEY REGION. *Scientific Publications of the Cleveland Museum of Natural History, Vol. IV, No. 1.*

By Harry C. Oberholser. Cleveland Museum of Natural History, Cleveland. 6¼ x 9¼; 12; 1932 (paper).

NEW MAMMALS FROM ST. LAWRENCE ISLAND, BERING SEA, ALASKA. *University of California Publications in Zoölogy, Vol. 38, No. 9.*

By E. Raymond Hall and Raymond M. Gilmore. University of California Press, Berkeley. 25 cents. 7⅛ x 10¾; 12 + 2 plates; 1932 (paper).

A NEW LAKE-SIDE POCKET GOPHER FROM SOUTH-CENTRAL CALIFORNIA, *by Joseph Grinnell.* A NEW POCKET GOPHER FROM NEW MEXICO, *by E. Raymond Hall. University of California Publications in Zoölogy, Vol. 38, Nos. 10 and 11.*

University of California Press, Berkeley. 25 cents. 7⅛ x 10¾; 10 + 1 plate; 1932 (paper).

BOTANY

ANTHOKINETICS. *The Physiology and Ecology of Floral Movements. Carnegie Institution of Washington Publication No. 420.*

By G. W. Goldsmith and A. L. Hafenrichter. Carnegie Institution of Washington, D. C. $3.00 (paper); $4.00 (cloth). 6¾ x 10; iv + 198; 1932.

Beginning their studies in each case with observations on floral movement in the field, Goldsmith and Hafenrichter proceeded to laboratory examination of nearly a hundred species, drawing their material from a mountainous region where a variety of types of floral behavior was to be found.

> Under constant conditions such as were employed in the present study, flowers generally show periodic opening and closing movements during the first 24 hours after removal from the field. That is, the general features of the daily behavior of these flowers were predetermined for at least one day after removal from the field and subjection to constant conditions. . . . . The strength of periodicity, as measured by the degree of maximum expansion and rate of movement under constant conditions and in response to temperature changes, differs greatly in the different forms. In the flowers of *Taraxacum* and similar forms, periodicity is strong and modifies all floral movements, even after the flowers have been kept under constant conditions for several days. In the flowers of *Tulipa*, periodicity is weak and can easily be overlooked since stimuli of moderate intensity entirely mask it.

The authors made detailed studies of the influence of temperature, light, and humidity on the opening and closing of flowers, but always with reference to their natural periodicity.

There is a rather complete literature review which helps to make this a valuable contribution to an old and honorable botanical problem.

METHODS IN PLANT HISTOLOGY. *Fifth Revised Edition.*

By Charles J. Chamberlain. University of Chicago Press, Chicago. $3.25. 6 x 8⅝; xiv + 416; 1932.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 389. Ernährung und Stoffwechsel der Pflanzen.* Containing following articles: *Methoden zur Untersuchung der Wasserverhältnisse von Torfböden,* by Karl Malmström; *Die botanisch-mikrotechnischen Schneidemethoden,* by Josef Kisser.

Urban und Schwarzenberg, Berlin. 9 marks. 7 x 10; 159; 1932 (paper).

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 393. Ernährung und Stoffwechsel der Pflanzen. Die botanisch-mikrotechnischen Schneidemethoden.*

By Josef Kisser. Urban und Schwarzenberg, Berlin. 11 marks. 7 x 10; 206; 1932 (paper).

The fifth edition of Chamberlain's textbook has been thoroughly rewritten and enlarged. Some new techniques for sectioning wood are described and there are new sections on photomicrography, including the use of motion picture equipment.

Kisser has prepared an exceedingly detailed description of the techniques of imbedding and section-cutting of plant material which should be very useful to any plant histologist. Fixation and staining are not discussed.

The methods of investigation which Malmström has developed for the study of peat soils should be useful in work on other soil types.

PLANT SOCIOLOGY. *The Study of Plant Communities. Authorized English Translation of Pflanzensoziologie.*

By J. Braun-Blanquet. Translated, Revised and Edited by George D. Fuller and Henry S. Conard. McGraw-Hill Book Co., New York. $4.50. 5⅞ x 9; xviii + 439. 1932.

Sometime when someone writes the much needed *Dictionary of Ecological Nomenclature*, it will have to be explained that the reason why a term like "sociology" was dragged in was that some ecologists who write textbooks are interested in such things as pollination and seed dispersal and that others aren't; the latter show their interest in plant communities by recourse to picturesque language. What Braun-Blanquet has done is to make a usable and important survey of the recent literature dealing with plant communities and the climatic and edaphic conditions that influence them, writing for advanced students of ecology. Not least of the merits of the book are a bibliography of more than 600 titles and a good index.

CONTRIBUTIONS DU LABORATOIRE DE BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL. Nos. 20–21. *No. 20: Quelques Plantes Nouvelles ou Reliquales du Bassin de la Baie des Chaleurs. No. 21: Sur Quelques Ptéridophytes Nord-Américaines.*

By Frère Marie-Victorin. University of Montreal, Montreal, 50 cents. 6 x 9; 29; 1932 (paper).

MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Volume XXIII, Nos. 134 to 138. Carnegie Institution of Washington Publication No. 433.*

Carnegie Institution of Washington. $5.00 (paper); $6.00 (cloth). 9 x 11⅝; iii + 266 + 26 plates; 1932.

This volume contains five papers. The first—Studies in the reproduction of the monkey *Macacus (Pithecus) rhesus*, with special reference to menstruation and pregnancy,—by Carl G. Hartman, is especially important. Over 700 menstrual cycles are recorded. It is found that ovulatory and non-ovulatory cycles are followed by approximately the same amount of bleeding, and that the same individual, with regular menstrual rhythm, may alternate ovulatory with non-ovulatory cycles. Ovulatory cycles are more prevalent in the winter than in the summer months, a fact which seems to demonstrate a breeding and a non-breeding season for the rhesus monkey. The optimum conception day is found to be the end of day 13 or the beginning of day 14. The gestation span was studied and found to vary with the physique of the individual—the more vigorous individuals keeping the fetus longer. The average period of gestation is 164 days.

The second paper, by George B. Wislocki—On the female reproductive tract of the gorilla, with a comparison of that of other primates—is also of great importance. The results of this study support the statement that, from the standpoint of reproduction, man shows the closest anatomical relationship to the anthropoid apes and not to the catarrhine or platyrrhine monkeys. The resemblance is closest in connection with the internal reproductive tract and with placentation.

The third paper—Observations on the bones of the skull in white and negro fetuses and infants—by Marciano Limson, presents the results of a study made of the significant variations and anomalies found in 163 skulls selected as showing no evident symptoms of disease of white and negro fetuses and infants. Anomalies are found to be much more common in fetuses than in adults. All of the variations and anomalies found in the fetuses are known to exist in adults, which suggests the conclusion that such conditions in adults originate during prenatal development.

The other papers in this volume are: The living egg and early stages of its development in the guinea-pig, by Raymond R. Squier; and A presomite human embryo with a definite chorda canal, by Chester H. Heuser.

PHYSIOLOGY AND PATHOLOGY

VITAMINS: A SURVEY OF PRESENT KNOWLEDGE. *Medical Research Council Special Report Series, No. 167.*

Compiled by a Committee appointed jointly by the Lister Institute and Medical Research Council. His Majesty's Stationery Office, London. 6s. 6d. net. 6 x 9½; 332; 1932.

This is the third survey on vitamins which has been issued by a committee appointed by the English Medical Research Council and the Lister Institute. The first is a *Report on the present state of knowledge concerning accessory food factors (vitamins)* and was issued in 1914. The second, a completely new edition, appeared in 1924. In the last survey, commenced in 1930, again a wholly new undertaking was necessary in order to keep pace with the rapid development of the subject. The report will be valuable to instructors, investigators and practicing physicians. The latter will find the sections on "Vitamins and human diets" and "Vitamins in the diet of mother and infant" especially useful. The survey has been made with care and is well documented. The list of references runs to something over 1,500 titles. In Appendix I will be found a table giving the distribution of vitamins in foodstuffs, etc. In Appendix II is given the "Report of the conference on vitamin standards held at London from June 17th to 20th, 1931." In the text are given photographic reproductions of children showing vitamin deficiency, growth curves, charts and tables. There is an index.

A REPORT ON TUBERCULOSIS *Including an Examination of the Results of Sanatorium Treatment. Reports on Public Health and Medical Subjects No. 64.*

By Arthur S. MacNalty. His Majesty's Stationery Office, London. 3 shillings net. 6 x 9⅝; viii + 172; 1932 (paper).

This is a comprehensive study of the present position concerning the prevention and treatment of tuberculosis in England, dealing especially with the sanatorium and the results of such treatment. In 1911 there were 53,120 deaths from tuberculosis. In 1930, there were 35,745. That the problem is one of great complexity and that the goal of complete success is not yet in sight this report deeply testifies. It is shown how contact infection, industrial occupations, urbanisation, overcrowding, poverty, lack of proper nutrition and other diseases favor tuberculosis, and how a return to natural conditions enables the human body to resist tuberculosis. The battle, however, against this devastating disease is not so simple as it was at one time thought to be. It is "only by co-ordinated progress along various paths and by surveying the complex problem as a whole that tuberculosis is likely to be combated successfully."

HANDBUCH DER BLUTGRUPPENKUNDE.

Edited by Paul Steffan. J. F. Lehmanns Verlag, München. 48 marks (paper); 50 marks (cloth). 6⅝ x 10; xi + 669; 1932.

A comprehensive review of the research on blood-groups which has been done since the discoveries of Landsteiner in 1901. The book is divided into nine parts. Dr. Michael Hesch contributes Part 1, on the development of research on blood-groups, and Part 9, a bibliography of about 3,000 titles. Part 2, on the serology of blood-groups of man and animals, is contributed by Oluf Thomsen; 3, on the inheritance of group determined properties of the blood, by Siegmund Wellisch; 4, the relations between blood groups and other hereditary characters, especially abnormal conditions, by Oluf Thomsen; 5, the practical significance of blood-group research in medical treatment, by Heinrich Bürkle-de la Camp; 6, the science of blood-groups in forensic medicine, by Gottfried Raestrup; 7, blood-groups and races of man, by Paul Steffan; and 8, the technic of blood-group determination, by E. D. Schött. In addition to the general bibliography there is, appended to Part 5, a list of over 200 titles dealing with blood transfusion. The book is well indexed.

EPIDEMIOLOGY, *Historical and Experimental. The Herter Lectures for 1931.*

By Major Greenwood. The Johns Hopkins Press, Baltimore. $1.50. 5¾ x 8¾; x + 80; 1932.

In the first of these lectures the history of epidemiology from Hippocrates to Ross and Brownlee is outlined. The second and third lectures are devoted to the author's pioneer work in experimental epidemiology, from which he concludes that "if

healthy immigrants are admitted to an infected herd, even if infected immigrants are rigorously excluded, the herd sickness will recur although intervals of apparent freedom may be so long that the disease will seem to have died out" and that "pre-immunised animals suffer a lower mortality than non-immunes, but that in a herd recruited wholly from pre-immunised animals the disease does not die out." Thus, while pre-immunisation is an invaluable means of reducing the mortality of persons exposed for a short time to great risks, it cannot take the place of environmental betterment. On the other hand, in virus as distinct from bacterial diseases there are reasons for thinking that active immunisation may be an effective prophylaxis.

The material is presented with great charm. It exhibits throughout the wide and profound range of learning, the sound critical judgment, and the polite but sometimes biting irony and wit, for which the author is famed. Altogether this little book is one to be read and pondered over by every public health official for its direct bearings upon his daily business; and by the investigator in any field of biology for its philosophical insight into the difficulties and limitations of scientific methodology.

Handbuch der Biologischen Arbeitsmethoden. *Lieferung 387. Allgemeine und vergleichende Physiologie.* Containing following articles: *Die Vitalfärbung des Blutes*, by R. Wolfer; *Die Schaukelextraktionsmethoden*, by Erik M. P. Widmark; *Methoden der Bauchfensterbildung*, by Josef Deutsch; *Mikrogeometrische Messung*, by Keijo Okajima.

Urban und Schwarzenberg, Berlin. 10 marks. 7 x 10; 150 + xx; 1932 (paper).

The articles in this number of the Abderhalden *Handbuch* series deal with the following subjects: the vital staining of blood; shaking methods of extraction (we found pictured one ingenious apparatus constructed from a boy's "Meccano" set); the construction of abdominal windows; and microgeometric measurements of organs and tissues.

BIOCHEMISTRY

The Donnan Equilibria *and their Application to Chemical, Physiological and Technical Processes.*

By T. R. Bolam. G. Bell and Sons, London. 9 shillings net. $5\frac{3}{8}$ x $8\frac{5}{8}$; vii + 154; 1932.

The intimate connection of the Donnan equilibria with biological processes may be indicated by a quotation:

> The theoretical considerations detailed in the following lead to the general conclusion that the presence in any system of electrolytes of a species of ion, which is restrained in *any* way from diffusing to all parts of the system, will give rise to unequal distribution of every species of diffusible ion present. This particular state of *unequal ionic distribution* is the characteristic feature of "Donnan equilibria."

Approximately a third of the book is devoted to biological applications of the equilibria. There is an adequate index and a bibliography of 143 titles.

The Biochemistry of Muscle.

By Dorothy M. Needham. E. P. Dutton and Co., New York. $1.25. $4\frac{1}{8}$ x $6\frac{5}{8}$; viii + 166; 1932.

A summary of recent discoveries about the process of conversion of chemical energy into the energy of muscle contraction. The author discusses the revolution in the old physiological views of muscle contraction, and the reinterpretation of facts, long known, into a new picture. Most of the chemical work described has been done on frog and rabbit muscle. The assumption is made that these observations can be generally applied to voluntary muscle. There is an extensive bibliography, a good glossary and an index.

Electrometric pH Determinations of the Walls and Contents of the Gastro-Intestinal Tracts of Normal Albino Rats. *University of California Publications in Zoology, Volume 36, No. 14.*

By Charles A. Kofoid, Ethel McNeil and Relda Cailleau. University of California Press, Berkeley. 25 cents. 7 x $10\frac{1}{4}$; 9; 1932 (paper).

Rats on a relatively low fat diet showed a

practically neutral reaction for the wall of the duodenum and ileum and a slightly alkaline reaction for the caecal wall. The rats tested were not examined for intestinal amoebae, but as other rats living in the same cages showed many amoebae and flagellates in the caecum the authors conclude that a neutral or alkaline range, approximately the pH of the blood, is optimal for the growth of these protozoa of the rat.

Wörterbuch der Kolloidchemie.
By Alfred Kuhn. Theodor Steinkopff, Dresden and Leipzig. 8 marks. $4\frac{3}{4} \times 7\frac{5}{8}$; 179; 1932.

This is something more than a dictionary; it is a sort of small textbook on colloid chemistry alphabetically arranged with graphs, tables, illustrations, and literature references, and it should make life considerably easier for any biologist reading up on colloid chemistry.

SEX

My Future Child and Yours. *An Intelligent Program of Improving Life at its Source, Before Conception and in the Womb, Written in a Simple Manner to be Understood by all.*
By Roscoe C. Evans. Roscoe C. Evans, Oklahoma City. $5\frac{1}{4} \times 7$; 238; 1931.

"Intelligent procreation" is the theme of this book. "Intelligent procreation consists" in recognizing, besides heredity and environment, prenatal influence as a third great factor influencing the development of individuals. Prenatal influence, claims the author, occurs whether we are conscious of it or not. The program of intelligent procreation is to influence the unborn child consciously, in the right direction, impressing on it good habits, trends and attitudes. This influence is to be accomplished through the agency of the mother's endocrine glands, but only as a result of both Papa and Mama taking thought and following the author's program of righteous, not to say pious living.

No book has depressed us so much as this in a long time. It has spoiled our day because it is so perfect an exemplification of two great and immutable truths: One, that honesty, sincerity and nobility of purpose are hopeless as substitutes for knowledge, insight and understanding, quite regardless of their value otherwise; the other, that a little knowledge is worse than a dangerous thing, it is devastating.

The Critical Age of Woman.
By Walter M. Gallichan. Williams and Norgate, London. 4s. 6d. net. $4\frac{7}{8} \times 7\frac{1}{8}$; 160; 1932.

The author discusses in non-technical language the physical and psychological problems which arise as woman approaches the so-called critical age and shows how neuresthenia and various forms of emotionalism seem to be directly traceable to the improper instruction of young girls in matters pertaining to sex physiology, to unhappy marriages, or unfulfilled desires.

BIOMETRY

Fertility and Reproduction. *Methods of Measuring the Balance of Births and Deaths.*
By Robert R. Kuczynski. Falcon Press, New York. \$1.85. $5\frac{7}{8} \times 9$; 94; 1932.

The experienced and well trained worker in population statistics can read this book without very much harm (except waste of time), for he can correct most of the author's numerous errors as he goes along. But when, on the first page of the text, the author states his purpose: "This book is intended to serve as an introduction into the methods of measuring fertility and reproduction," the unsuspecting beginner deserves a warning against the pitfalls prepared for him. Some of these are mere inaccuracies of algebra, as when, on pages 28, 29, 30, 57, 85, 86, 87, 90, and 91, for example, the wrong sign is attached to certain quantities; or when a formula is plainly garbled, as in the last formula on page 86.

More serious than these formal errors is the muddled thinking which has inspired such passages as the following: On page 28 the net reproduction rate (denoted by R_0) is defined as "female births per female

in stationary population." This statement taken literally has no definite meaning at all, because it does not state the length of time referred to. The reader will naturally suppose, in the absence of any other indication, that the annual births are meant. On this understanding the statement is plainly wrong, for actually the annual number of births per female in a stationary population is the reciprocal of the mean length of life, a figure of the order of .02, whereas R_0 is the ratio of births in two successive generations, a figure which, as a rule, will not depart materially from unity, and which has intrinsically nothing to do with the stationary population. What the author *meant* to say is "female births issuing from a life table cohort of females *in the course of its entire career*, per female entering the cohort at birth." Again on page 34 it is stated that the rate of increase of a stationary population dropped from 10.6 to 6.2 per 1,000. This is plainly nonsense. Another bad blunder is on page 58, last paragraph. The quantities R_1 and R_0 are completely determined by the life table and the age schedule of fertility, and since these are assumed given and constant in the discussion, the ratio $\frac{R_1}{R_0}$ cannot assume two different values, as it is here stated to do.

On page 26 the section "Yearly Rate of Increase Versus Yearly Increase" begins with a muddled title, continues with unnecessary complications, and ends without mentioning the one really significant fact, namely, that a rate of increase computed simply on the basis of the arithmetic mean of the population at the beginning and the end of the year comes within one in 30,000 of the answer found by Kuczynski's complicated formula.

But the prize for confusion of thought belongs, perhaps, to a passage on page 23, where the author remarks: "It is evident, therefore, that if a population is constantly subject to a certain mortality (in each year of age), and if the number of births constantly equals the number of deaths, this population, whatever may be its present age composition, will sooner or later have an age composition corresponding to that of the life table, and from then on will forever preserve this age composition." The fact, of course, is that under the conditions stated the population actually *is* stationary and it is only by the most extraordinary and improbable compensatory fluctuations in the age-specific fecundity that any other than the stable age composition could exist from the very start.

On pages 63 to 64 the author spends nearly a whole page expatiating on an alleged error of Dublin and Lotka, who, in their original paper on the *True Rate of Natural Increase* did not correct their population to the midyear number in computing their fecundity rates. Kuczynski speaks of this as a "serious mistake." The neglect, of course, is not a mistake at all, but the disregard of a minor factor in a computation which, in the nature of things, cannot be very accurate. But the singular thing about this incident is that Kuczynski himself, in another place, omits the corresponding correction in computing fecundity rates for Italy.

The account of Bortkiewicz's 1911 publication (*Die Sterbefrequenz etc. in der stationären und in der progressiven Bevölkerung*) and Lotka's 1907 papers (*Science*, Vol. 26, page 21; *American Journal of Science*, Vol. 24, page 199) and their relative contributions to the subject is wholly misleading. Bortkiewicz did *not* show, (as Kuczynski says he did), how to compute a stable age distribution. To do this requires the determination of the rate of natural increase corresponding to a given mortality and fecundity, and this is found for the first time in the literature in Sharpe and Lotka's paper in the *Philosophical Magazine* of April, 1911. Bortkiewicz did not "start from a stationary population and show what will be its ultimate composition," as stated by Kuczynski on page 41. What Bortkiewicz did show was how to compute the age distribution in a population that *has for years past been* growing in geometric progression, and in this he is quite clearly anticipated by Lotka, 1907. The formulae which Kuczynski refers to as Bortkiewicz's in contrast with Lotka's are all to be found in Lotka's 1907 paper, if allowance is made for perfectly obvious changes in notation and for the use of equally obvious finite summation in place of integrals, such as

inevitably follows in dealing with arbitrary functions.

Kuczynski's recommendations on page 90 regarding the use of what he distinguishes as Bortkiewicz's and Lotka's formulae are baseless, as he has quite failed to grasp the purpose of certain of these formulae, and has equally failed to recognize the identity of others where the two authors differ only in the notation employed. Lastly, to quote only one more of many misleading statements, Kuczynski, on page 91, remarks "whoever does not want to use Lotka's complicated formula . . . must resort to the formula

$$r = \sqrt[\frac{R_1}{R_0}]{R_0} - 1$$

It is significant that Kuczynski quite forgets to state here that the formula so recommended is also Lotka's.

Körperproportionen und Kopfform bei Neugeborenen.

By Erica Kugler. Art. Institut Orell Füssli, Zürich. $6\frac{3}{4}$ x $9\frac{5}{8}$; 149 + folding chart + 3 plates; 1932 (paper).

For this inaugural dissertation measurements were made on 500 new-born infants —250 boys and 250 girls— delivered in the Women's Clinic of the University of Zürich. The descriptions of the methods used in taking the various body and head measurements are augmented by some photographs. Tables give the body measurements and indices, head measurements and indices for each infant in the study. Among the conclusions the author reached are the following:

Body length of new-born boys is greater than that of girls. Number of birth and age of parent influences the body size of the new-born; the first-born is usually smaller at birth than later children. Legitimate children are larger at birth than illegitimate. There is no difference in the absolute leg length of boys and girls, but relative to the trunk length the legs of girls are longer than those of boys. The new-born are mesocephalic. Measurements made on the ninth day showed that the skull configuration had regressed considerably, as in this short space of time all head measurements, with the exception of height of face and breadth of the lower jaw bone angle had increased. There is a bibliography.

Anthropometry of Adult Maya Indians. *A Study of their Physical and Physiological Characteristics. Carnegie Institution of Washington Publication No. 434. Paper No. 38 of Department of Genetics.*

By Morris Steggerda. Carnegie Institution, Washington. \$1.25 (paper); \$1.75 (cloth). 7 x 10; iv + 113; 1932.

This study presents a mass of carefully collected anthropometrical data, which has been subjected to the usual biometric treatment. Seventy-seven males and 56 females were measured by the author, thus bringing the total number of Mayan males from whom physical measurements have been obtained up to 600, and females up to 450. The Mayan Indian is in general very stocky. Relative to Jamaican negroes and the descendants of the Dutch Frisian whites who settled early in that region, the Mayan has the broadest chest, the longest lower arm relative to total arm, the broadest hands, the broadest head and face, and the narrowest ear. His metabolism is highest, his pulse rate lowest, and he has the best teeth. There is a series of good photographs and an index.

PSYCHOLOGY AND BEHAVIOR

Death in the Afternoon.

By Ernest Hemingway. Charles Scribner's Sons, New York. \$3.50. $6\frac{1}{4}$ x $9\frac{1}{8}$; 517; 1932.

It has long been plain that there is great need for a thorough and comprehensive treatise on the psychobiology of the bull fight. A first class bull fight, with a good bull and a good matador supported by a competent *cuadrilla*, presents an opportunity not elsewhere paralleled to study some of the most profound problems of behavior, both human and animal. The situation is one of conflict, with death and its avoidance as the supreme motivation. Every form of mental activity—cunning, judgment, strategy, reflection, fear, cour-

age, and all the rest—is brought into play. Their resultants are translated into overt physical behavior in such manner as to be perfectly clear to the understanding observer, and all at such a *tempo* that an afternoon will give the philosophical behaviorist material for a month's reflection.

Unfortunately the complete biological treatise on bull fighting has yet to be written. But Mr. Hemingway's *Death in the Afternoon* comes nearer to supplying the deficiency, so far as concerns the English speaking world, than anything hitherto available. To be sure he is not a trained biologist, and consequently has perhaps not fully grasped the significance of some things and wrongly distributed the emphasis about others, but he is a grand *aficionado*. He knows his bull fights and fighters as probably no other Nordic ever did. Furthermore he has done a thorough and scholarly job in this book. It is logically arranged, well documented, supplements the text with pertinent and well executed illustrations, has a superb explanatory glossary of technical terms, and only fails to reach the highest standards of scientific bookmaking in its lack of an index. Furthermore Mr. Hemingway knows his material and its literature at first hand. He has watched and studied thousands of bull fights, and has not only read the book literature on the subject, but also the Spanish journals edited for fans over a period of many years back. He apologizes to competent *aficionados* for the elementary character of many of his explanations, but surely this is unnecessary. We need an elementary textbook before a pedantic monograph.

Hemingway interprets the bull fight, as a whole, from the artistic viewpoint. He sees in it the classical tragedy, its comedy relief furnished by the horses and the picadors, building up a gradual *crescendo* to the climax in the death of the bull. With great plausibility he fits everything that happens into this scheme. But, speaking as one *aficionado* to another, we feel that he would be the first to admit that other equally logical interpretations of the whole performance are possible. For example, the biologist might consistently and logically interpret the formal bull fight as the foreshortened and partly symbolic picture of the life cycle—the struggle for the continued existence of individual and race, wherein the individual fights to keep alive until he has planted the seed for the next generation, but in the end inevitably dies. On this view the charge of the bull at the horse is symbolically substituted for the sexual act, which even in animals is always slightly ridiculous in seeing, and is in fact at once the most thrilling depiction of that tremendous surging virility of the male which keeps the race going, and also the most stirringly erotic action that respectable ladies are anywhere permitted to witness. Were this not a family magazine detailed evidence could be offered in support of this latter point, derived in part from the reactions of the spectators. It is unnecessary to pursue the point further. We want merely to illustrate the wealth of material for the inquiring mind offered by bull fighting and Hemingway's book about it.

Any book by Hemingway needs no recommendation to the general reader. But we do want to recommend this particular book to biologists. It will give them a lot to think about. Until our own treatise on the *Biology of Bull Fighting* appears—and pressure of other work necessitates the postponement of its writing to our declining years which are already in part mortgaged to the bringing out of a projected *Natural History of Copulation* in elephant folio with numerous plates—we predict that Hemingway's will remain the unchallenged standard work on the subject.

Phantom Fame. *The Anatomy of Ballyhoo. By Harry Reichenbach as Told to David Freedman. Noel Douglas, London; Simon and Schuster, New York.* 7s. 6d. net (England); \$2.50 (U. S. A.) $5\frac{1}{4} \times 8\frac{1}{2}$; 258; 1932.

This amazing autobiography of the late Harry Reichenbach, "the greatest press agent in America" is not only intensely interesting reading, but also a revealing and almost incredible document on human psychology and behavior. It is the delineation of a career, starting in circuses, street carnivals, and such like shows; and cul-

minating in international recognition in the fields of publicity and organized propaganda. Harry Reichenbach developed his own knowledge of ballyhoo, "the gentle art of fooling the other fellow." He operated on the simple but sound hypothesis that in this day and age the success of any project or person is determined less by inherent capacity or quality than by properly manipulated publicity. On this philosophy he became the most valuable press agent of the infant motion picture industry. His activities in this connection, especially in raising unknown actors and actresses to stardom are particularly illustrative of how potent publicity can really be. He gives an interesting account of the reactions of the stars to their publicity-built reputations—their phantom fame; of the inflated egos which appear, the temperaments which develop and the recourse some take to liquor and drugs. In Chapter XII a keen analysis of the power of publicity is given, showing how, by means of press, radio, and film it is possible for 50 people in a metropolis like New York City to dictate the customs, trends, fads and opinions of an entire nation of 120,000,000 people.

The final chapters describe the activities of Reichenbach, and the part of publicity and propaganda in the World War. In the conclusion, David Freedman, his collaborator, writes of him:

> He always kept in the background and was scarcely known by the public at large, but in the arts and industries where he operated, his name was a magic key to all the mysteries of building fame and fortune from the printed word. The motion picture industry is inconceivable without him. . . . . He transformed the rudimentary principles of ballyhoo enunciated by Barnum and other circus pioneers into a philosophy of propaganda.

A grand picture of a great man, the perfect exemplar and fine flower of the civilization that nurtured him!

Konnersreuth. *A Medical and Psychological Study of the Case of Teresa Neumann. By R. W. Hynek. Translated and adapted by Lancelot C. Sheppard. Burns Oates and Washbourne, London; Macmillan, New York.* 4 shillings net (England); $1.50 (U. S. A.) $4\frac{5}{8} \times 7\frac{1}{4}$; v + 150; 1932.

Remarkable things have been happening to Teresa Neumann, a Bavarian peasant woman and a devout Catholic, ever since she injured her spine in 1918 at the age of twenty. They include a fast of five years duration; the periodic occurrence of raw, bleeding wounds on hands, feet, side, and face every Friday; visions; trances in which she speaks grammatically (more than can be said for Teresa's use of her native language), in a dead language, Aramaic, and a dozen more ordinary calamities.

Her original injury was aggravated by neglect and intensified by a series of severe accidents which finally left her paralysed and blind. Her recovery from this unhappy state is no more remarkable than some of the cures attributed to her. The wounds which appear at the time when she sees visions of the crucifixion of Jesus, bad as they are, are really among the least of her infirmities. The visions are described so vividly and with such a wealth of gruesome detail that at times we were not sure who saw the visions, Teresa or Dr. Hynek.

Since 1927 Teresa has taken no food or drink, except the daily communion. Dr. Hynek stresses the point. On one occasion for two weeks she was kept under continuous observation by four nuns who swore that during that time she received only 39 grams of bread and 45 cc. of water and at the end she weighed exactly as much as she did at the beginning of the two weeks.

If this doesn't interest you in Teresa it surely ought to interest you in Dr. Hynek; he believes all this, and more.

The Psychological Effects of Menstruation.
By Mary Chadwick. Nervous and Mental Disease Publishing Co., Washington and New York. $2.00. $5\frac{7}{8} \times 9$; 70; 1932.

We deplore such an extreme Freudian approach to a subject which has not been adequately studied, and about which there exists such a vast amount of pseudoscientific talk. Such quotations as the following make us view the work with scepticism:

> The onset of puberty and the appearance of the menstrual flow awaken former guilt and phantasies

of castration and death to the child, with feelings of hostility to the mother and love to the father, normally, but occasionally this will be reversed. What influence may this have for the subsequent nervous development of the adult woman?

Further the author says:

By way of illustration of some of the points mentioned in this paper, we may include two case histories, which show in their prevailing symptoms, phantasies, dreams and transference manifestations, many of the same phenomena that were considered typical of those women, who were accused of witchcraft, as well as those characteristic of the related overwhelming mother-fixation.

It would be nice to have a sample somewhat larger than two.

PRINCIPLES OF MENTAL DEVELOPMENT. *A Textbook in Educational Psychology.*
By Raymond H. Wheeler and F. Theodore Perkins. Thomas Y. Crowell, New York. \$3.75. $5\frac{1}{2} \times 8\frac{1}{2}$; xxvi + 529; 1932.

This textbook aims "to present a Psychology for Education which relates the facts of experiment to the demand of the growing mind to live not only efficiently but with artistic and moral expression." The authors emphasize the fact that

"Psychology has yet to realize that it is the Science of Human Nature, not the science of sensations, reflexes, mechanical conditioning processes and bundles of urges" .... "that man is NOT a machine,"

and

"that the laws of his behavior are the laws of intelligence, will and personality, not the laws of association."

This will be found to be an exceedingly interesting and well balanced book, one in which the authors have not complicated but clarified the situation. Much previous experimental work is evaluated in the light of recent trends of psychological interpretations. Many will disagree with some of the main tenets which the authors hold and future studies will undoubtedly demand a new outlook on this exceedingly complicated subject, but the book trends in the right direction. Each section is well documented, the illustrations are adequate, and there are author and subject indices.

FLUCTUATIONS IN HUMAN OUTPUT. *The British Journal of Psychology Monograph Supplements XVII.*
By S. J. F. Philpott. Cambridge University Press, London. 12 s. 6 d. net. 7×10; viii + 125; 1932 (paper).

The problems discussed here are of fluctuations or oscillations in uninterrupted mental work. With the best of intentions, output fluctuates, and these fluctuations can be measured experimentally. The general hypothesis of the study is that output curves are essentially periodic, the waves being geometric in nature, i.e., of constant periods when plotted against the logarithm of time. Evidence in support of this periodicity is presented, and interrelationships between the various wave measures noted. The results seem to substantiate the hypothesis, and the further more fundamental conclusion is drawn that

there are many elementary waves present, their logarithmic periods being whole-number multiples of a given (but as yet unmeasured) unit of logarithmic time, that the said unit is universally true for all our subjects, under all conditions of experiment met with, and that finally, true phase differences from curve to curve seem to be negligible.

There is a bibliography of 37 references.

THOSE SUPERSTITIONS.
By Sir Charles Igglesden. Jarrolds, London. 6 shillings net. $4\frac{3}{4} \times 7\frac{1}{4}$; 240; no date.

This is an amusing catalogue of superstitions common in English-speaking countries. Sir Charles is content to take his tales as he finds them, without criticism or comparison with the superstitions of other races. He is inclined to think many superstitions were originated for personal profit by the witches who were hunted so relentlessly in former times. The foreword contains the warning:

When the legend of hell fire, eternal and actual, fell to pieces, many an honest man's trust in Heaven went with it. We must be careful how we destroy superstitions lest we undermine the very supports which hold above the earth all those who do "not live by bread alone."

An Elementary Psychology of the Abnormal.

By W. B. Pillsbury. McGraw-Hill Book Co., New York. $3.00. $5\frac{1}{2}$ x 8; x + 375; 1932.

The aim of this book is to give the college student and the general reader an account of those aspects of abnormal psychology that are likely to affect or interest them. The facts and theories of hypnotism, the neuroses, insanity, and feeble-mindedness are presented. There is a concluding chapter on mental hygiene. Like many other academic psychologists the author is critical of Freud and his work.

Gorillas in a Native Habitat. *Report of the Joint Expedition of 1929–30 of Yale University and Carnegie Institution of Washington for Psychobiological Study of Mountain Gorillas (Gorilla beringei) in Parc National Albert, Belgian Congo, Africa. Carnegie Institution of Washington Publication No. 426.*

By Harold C. Bingham. Carnegie Institution of Washington, D. C. $2.00 (paper); $3.00 (cloth). $6\frac{3}{4}$ x 10; ii + 66; 1932.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A History of Fire and Flame.

By Oliver C. de C. Ellis. Simpkin Marshall, London. 15 shillings net. $4\frac{5}{8}$ x $7\frac{1}{2}$; xxiv + 440; 1932.

Intelligent men in other times than our own have felt more or less clearly the need for fundamental concepts akin to our ideas of solid, liquid, gas, and energy, and to fill this need they have evolved a bewildering variety of concepts, related, so Dr. Ellis implies, by a common necessity for clarity in thinking about nature. These concepts did not remain the property of wise men and natural philosophers; they were taken over by the common people, distorted and given new values, and the properties, real and imaginary, of earth, water, air, and fire (the fore-runners of our physical concepts), became matters of ritual and belief and so shaped human conduct mightily. Ellis has undertaken to show, by collecting and collating bits from the literature of antiquity, fragments of folk-lore, and materials with which the scientific community is more familiar, how these fundamental concepts developed. No other kind of book, except a dictionary, could refer learnedly to as many kinds of knowledge in one volume as this one. Suppose, for instance, we list the items that fall under Q in his index: Quakers, qualities, Quanta, Quantitative treatment, Quenching, Quern, Quetzalcoatl, Quicksilver, Quiller-Couch, Quills, and Quintessence; there are about 5000 other items in the index as diverse as these. His concluding chapters deal with modern views on the nature of flame and explosions and are illustrated by photographs of exploding gas mixtures taken at 20 millisecond intervals.

We have tried to outline the central thesis of the book, but it would be misleading to say it is the most important feature, either to Dr. Ellis or to the reader. It so happens that the pleasantest feature of the book is the same one that makes it hard to follow; an uncontrollable tendency to wander away from the argument into a maze of anecdotes, extended quotations from mediaeval treatises, and little oddities of all descriptions. It wouldn't be the entertaining book it is without this glaring weakness.

Pistol v. Poleaxe. *A Handbook on Humane Slaughter.*

By Lettice Macnaghten. Chapman and Hall, London. 21 shillings net. $5\frac{1}{2}$ x $8\frac{1}{2}$; xxv + 577; 1932.

A comprehensive and well-illustrated book in which the author has summarized almost all of the literature which has appeared in the last twenty years on the subject of humane slaughter of food animals, and puts in her plea for the compulsory use of humane killing instruments in Great Britain. Although many towns in Great Britain have passed laws on slaughter-house reform and the pistol is in pretty general use where cattle are killed, there are still a large number of towns which refuse to do so. This is especially true in districts where large numbers of sheep and pigs are killed as it has been found to be

almost impossible to adopt mechanical stunning before cutting the throat of the animal on account of the "splashing" which occurs in a high proportion of cases, and because of the difficulties which are met with in the curing and preservation of the flesh. These difficulties have been overcome in Continental Europe where an electric device is being used with some success. This device has the added advantage of doing its work silently—even on pigs. However, Miss Macnaghten concludes her views, given in the introduction, as follows:

> *Attempts are made from time to time to put on the market mechanical killers which are attractive to the* trade because they require no cartridge, or for some other reasons. If these killers are passed by the Societies for the Prevention of Cruelty to Animals, we may well rest content. If not, we should demand an investigation, and in the event of the killer not being considered satisfactory, we must press for the old and reliable types to be substituted.
>
> Stunning by electricity is hardly mentioned in this book. My own view is that we already have safe, simple, economical and perfectly humane killers for all requirements. Why trouble about another method, the action of which has the reputation of being most uncertain?

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THE QUARTERLY REVIEW of BIOLOGY

THE PROBLEM OF ACQUIRED PHYSIOLOGICAL IMMUNITY IN PLANTS

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I. INTRODUCTION

A KNOWLEDGE of the principles underlying the reactions of a host attacked by a parasite has been of inestimable value in the understanding and control of human diseases. So, too, phytopathology has found that the study of immunity and susceptibility has made possible much of its progress in recent years. Three of the major advances in the present century in plant pathology are closely dependent upon a knowledge of the factors of immunity and susceptibility, namely, the breeding for disease resistance, the discovery of the significance of biological races, and the study of the effect of environment upon plant disease. The ability of the animal to resist infection by the acquirement of a state of partial or complete immunity, contingent upon sensitization by the parasite, is the basis of the most important recent advance in medicine, serotherapy. Accordingly, plant pathologists have not failed to recognize the important theoretical and practical advantages of a knowledge of the rôle of acquired immunity in plants. As early as 1901 Ray and Beauverie offered the first suggestions regarding a display of immunological reactivity in plants comparable to that in animals. Many other plant pathologists, physiologists, and geneticists have since considered this possibility in theory, in observation, and in experiment.

This type of work is comparatively unknown to American investigators which is due, in part at least, to the fact that there has appeared no adequate analysis of this field of study in English. The writer, when questioned regarding acquired immunity in plants has repeatedly been forced to direct his interrogators to the excellent monograph of Carbone and Arnaudi (47), which being in Italian cannot be studied freely by most American botanists. To the intensive student in the field of plant immunity this work is a most valuable contribution, but to the botanist who does not specialize in immunology yet who wishes to be informed upon this subject, the work of Carbone and Arnaudi is usually assimilated with such difficulty

that it fails to afford the practical answer to the inquiring American botanist.

The problem of acquired immunity in plants is rapidly passing its orientative stage. It is accordingly imperative that our knowledge in this field be reduced to a tangible and assimilable basis which will serve both to stabilize this branch of plant pathology and to guide future investigation in the field. Since the appearance of the monograph of Carbone and Arnaudi several important contributions in acquired plant immunity have lent new viewpoints to the problem, and these tend to modify our conception of the significance and value of the field.

There has been evident a growing tendency for pathologists to attribute observations of various nature to acquired immunity in plants. Unfortunately such points of view are frequently based on no experimental evidence and merely represent analogy. Without any available and adequate critique of the subject to act as a stabilizer of such theory, this tendency to unconstrained comparison has led many botanists to wholly erroneous conclusions regarding the rôle of acquired immunity in plants. The expressions of human serology have been applied to the most heterogeneous plant phenomena *ad libitum* until there is a grave danger that the few really valuable findings in this field may be lost in an inextricable maze of speculation and insufficiently grounded hypothesis. Such erroneous comparisons are rendered particularly confusing by the lack of discrimination in the employment of serological terminology to plant phenomena of obviously distinct nature. The indiscriminate use in plant reactions of such terms as *antigen*, *precipitin reaction*, and *antitoxin* in view of their precise and restricted meanings in serology, leads the average botanist to assume that there is evidence that such phenomena are *homologous* in the two fields, whereas in many cases such "homology" is merely a superficial analogy.

During his investigations in plant immunology the writer has felt it necessary to assemble and survey all of the available work bearing upon this problem. For the reasons outlined above it has been suggested that the results of this survey be made available to American investigators. The present paper is accordingly designed to meet the need for such information by rendering accessible and digestible the mass of accumulated evidence regarding the immunological behavior of plants, analyzing the present status of the subject together with the contentions which have been adequately demonstrated or refuted, and from the results of this analysis indicating the direction of future research in this field.

II. IMMUNOLOGICAL CONCEPTIONS AND TERMINOLOGY

In order to have a basis for a clear understanding of the problem of acquired immunity in plants it is first necessary to understand the various concepts and terms of immunology as they apply to plant phenomena. That a plant may be successfully invaded by a parasite it must possess a greater or less degree of *susceptibility*. The converse of susceptibility, i.e. the ability of a plant to withstand parasitic invasion, is *resistance* or *immunity*. These last two terms, however, have come to have distinct meanings in plant immunology. Fischer and Gäumann (64) very wisely limit the expression *immunity* to phenomena of the type of the reactions of animals to infection, i.e. to the ability of withstanding infection acquired by the host as the result either of stimulation by the parasite or of the introduction of protective substances. *Resistance*, on the other hand, applies to the congenital

capability of a plant to withstand parasitic attack. Resistance and immunity may be of various types. In the first place they vary greatly in degree. Absolute susceptibility, resistance, and immunity are comparatively rare, these properties being relative. We speak of certain grains as being resistant to the wheat rust. Actually the rust mycelium is able to penetrate the tissues of such resistant hosts but is unable to establish a permanent nutritional régime; the host is accordingly not absolutely but practically immune. Susceptibility and resistance or immunity may be generalized through the whole plant body or may be localized in certain tissues. Susceptibility or resistance may extend in duration throughout the life of the plant or may be temporary, at some one stage of development of the host. Both may be profoundly influenced by the environment. Immunity may be specific, directed toward a single type of organism employed in immunization, or may be non-specific or general, directed against a wide range of parasites. Resistance and immunity may be anatomical or morphological in character, or on the other hand they may be of a chemical or physiological nature. Finally, chemical or physiological immunity in the sense defined above may be either passive, static, due to the introduction of protective substances, as in human medicine by the injection of antitoxins, or on the other hand active, dynamic, due to the elaboration by the host of protective substances as a result of stimulation by the parasite, as in the immunity acquired by man as the result of an attack of smallpox.

In order that parasitism be successful the parasite must accomplish three ends: (a) It must penetrate to a suitable infection court; (b) it must establish a satisfactory nutritional régime; and (c) it must resist attempts on the part of the host to restrict or destroy it. Susceptibility depends upon the accomplishment of all these ends. Immunity, in our sense, consists in the breaking of this course at the last point.

The present paper deals with acquired physiological immunity in plants. From the foregoing analysis of the terminology we may now define this expression as the capability of withstanding infection acquired by the host either through the introduction of protective chemical substances of biological origin (passive), or through the elaboration of such protective substances in the host as a result of stimulation by the parasite. While the expressions host and parasite have been used throughout the discussion above, it must be understood that the same principles as apply to the host-parasite relationship apply also to the relation between two symbionts or between a plant and introduced substances of a stimulative nature, such as toxins or proteins which if not counteracted or inactivated would have a deleterious effect upon the plant.

The mechanisms of acquired physiological immunity in animals are the *antibodies*. This term applies to chemical substances of biological origin which have the function of neutralizing or counteracting the introduced protein or other foreign body, which latter stimulating agents are known as *antigens*. The term antibodies is not to be understood as applying to substances of well defined composition, since their nature has never been fully understood in animal serology. Antigens appear to be large colloidal molecules, and are probably chiefly or entirely protein in nature. The antibodies may be *normally* present in the blood of non-immunized animals or they may be present only as the result of stimulation by introduced antigens (*immune antibodies*). The antibodies are demonstrated by a number of types of reaction, although it is not certain as yet whether

these different types of reaction are due to different manifestations of the same antibody or whether different types of antibody are responsible for them.

The major types of reaction are briefly characterized as follows:

1. The *precipitin reaction* is due to the precipitation of a soluble antigen by the antibodies, here called *precipitins*, in the blood of animals immunized against the specific soluble antigen.
2. The *agglutinin reaction* occurs when the antigen is not soluble but in the form of discrete and visible particles, such as bacteria, blood corpuscles, or in plants possibly as plastids or pollen. It is due to the action of antibodies known as *agglutinins* and results in a clumping together of the foreign bodies and the consequent inactivation of the latter.
3. The *toxin-antitoxin reaction* is the neutralization of an introduced poison (*toxin*) by antibodies here known as *antitoxins*. Introduced toxins may be either antigenic (as many bacterial products) or non-antigenic (as certain mineral poisons).
4. *Anaphylaxis* is an immune reaction in which an organism inoculated with an antigen shows violent symptoms of distress upon the introduction of a second, very small dose of the same antigen after an interval of time in which *sensitization* to the antigen has occurred.
5. *Lysis* is the dissolution of non-soluble or soluble antigenic material by antibodies here known as *lysins*. It customarily takes the form of the disintegration and solution of bacteria or corpuscles in the presence of immune serum, and according to the type of antigen broken down may be variously designated as *bacteriolysis*, *hemolysis*, *cytolysis*, *proteolysis*, etc.
6. *Phagocytosis* is a manifestation of immunity in which certain specialized cells of the body (*phagocytes*) are able in an amoeboid fashion to engulf and digest invading organisms, in particular bacteria. It is more a function of congenital than acquired immunity.
7. *Mithridatism* (from Mithradates VI, king of Pontus, who was believed to have so saturated his body with poisons that he was immune to poisoning) or *habituation* is much less truly an immune reaction than the other types of immune reaction listed above, since it is much weaker and less specific than the other reactions. It is exemplified in the tolerance shown by chronic addicts to narcotics and by animals treated with increasing doses of certain non-antigenic poisons, such as arsenic.

This outline, in the preparation of which the writer is particularly indebted to the monograph of Wells upon the chemistry of immune reactions (185), is in brief a statement of the terminology of animal immunity. In animal immunology the customary sequence of events is as follows: An antigen is introduced into the blood system of an animal. This antigen may be soluble, as egg albumen, or particulate, as in the case of foreign blood corpuscles or bacteria, and in the latter cases may be of a virulent strain, producing a severe attack of disease, or a non-virulent or attenuated strain, producing a mild symptomatic display (*vaccination*). After a given period of time during which antibody-formation occurs, the blood of the immunized animal is withdrawn, clarified,

and tested against the antigen (usually with dilution and incubation at 37°C.). Immunity is manifested by a precipitation or cleavage of the antigen if the latter is soluble, by agglutination or lysis of particulate antigens, or by a combination of these reactions. These reactions are usually specific, i.e. positive in high dilution only toward the specific antigen used in the original inoculation. The antibodies are usually characterized by thermolability, activity in very high dilution, dependence upon the presence of electrolytes, and behavior as colloids in regard to electrical fields and dialyzing membranes.

As the result of the production of such antibodies the animal has now become immune in greater or less degree toward the antigen. If the antigen was a poison a large dose no longer exerts the same toxic effect as it would have in the non-immunized animal. If the antigen was a pathogenic organism it is no longer able to produce in the host the same severe pathological effects as it could originally have produced. If the immunity has resulted from an infective attack, the animal either recovers or its symptoms are at least ameliorated. If the antigen was in the form of a vaccine, the host is no longer highly susceptible to virulent attacks of the pathogenic organism. The serological display is hence causatively associated with pathological phenomena and the two types of effects serve to explain each other.

Now from the foregoing analysis it becomes apparent that any application of the zoöimmunitary concepts and terminology to plant phenomena must of necessity involve reactions homologous in the two kingdoms. Every precipitate observed in plant fluids is not a "precipitin reaction," but only such precipitates as are due to *precipitins* in the zoöimmunitary sense, acting in essentially the same fashion as zoöprecipitins; every clumping of bacteria or plastids in plants or plant fluids is not an "agglutination," but only such clumping as is due to the action of *agglutinins* in the sense of serology.

It is certainly not to be understood that all reactions of plants of an immunological nature must necessarily be of the same types as the serological reactions. The differences in gross physiology might well lead to different types of immune reactions in plants and in animals. Thus the inhibition of fungus spore germination or the modification of mycelium *in vivo* have no exact counterpart in serology, yet they doubtless play an important rôle in phytoimmunity. Hence a rigid adherence to serological nomenclature will not only lead to false homologies but will needlessly restrict the terminology of phytoimmunity, and it is accordingly here emphasized that serological nomenclature be applied to plant immunology only where there is definite proof that the reactions described are of the same type, and that it be openly recognized that there may be in plants immunological phenomena having no counterpart in serology due to the gross physiological differences in plants and animals, and that such phenomena demand investigation and discussion as unique plant problems, unhampered by an artificial attempt at homology with zoöimmunitary concepts and terminology.

III. THE DEVELOPMENT OF THE CONCEPTION OF ACQUIRED IMMUNITY IN PLANTS

Having an understanding of the conceptions and terminology of immunology as an aid in discussion of the subject, it is now possible to pass to a consideration of the contributions which have been made in this field. This may best be accomplished first by briefly reviewing in a chronological manner the main steps in the progress of the development of the problem, and then passing to a detailed account of the theories

and findings in the various branches of the field. Accordingly the present section will be devoted to such an account.

The studies in acquired immunity in plants were inaugurated by the reports of Ray (147) and Beauverie (10) in 1901 of successful vaccination of certain plants against fungus diseases. In 1903 Hiltner and Störmer (74) and Süchting (169) advanced the hypothesis that the morphology and behavior of the root tubercle bacilli of Leguminosae are controlled by an acquired immunity of the leguminous symbiont. Two years later Schiff-Giorgini (155) came to the conclusion that the olive tree resists the attack of bacteria in the tubercle disease by the active production of antibodies. Meanwhile Bernard had been carrying on studies on the reasons underlying behavior in mycorrhizae, and in 1909 (16) published a complete account of the display of acquired immunity in the orchid mycorrhiza. Bernard's studies were also continued in subsequent years. Tischler in 1911 (170) suggested that the recovery of *Euphorbia* from a rust disease was due to acquired immunity of host against parasite. Brierley in 1915 (26) believed the same explanation was applicable to recovery of mosaic-diseased tomato plants. The following year Heinricher (71) suggested that pear may acquire an immunity to the mistletoe, *Viscum album*, an observation which he later confirmed in 1929 (72). Similarly Montemartini in 1918 (121) advanced the theory that oak may recover from attacks of the mildew through mechanisms of acquired immunity, an hypothesis which he supported with experimental proof in 1930 (122).

In the same year appeared the first of Magrou's studies on acquired immunity in mycorrhiza (110), the forerunner of several such works by the same investigator. Picado, in 1921 (141) reported the demonstration of acquired and specific agglutinins and lysins in a number of plants, while Lumière and Couturier, also in 1921 (106), believed they had observed anaphylaxis in plants. The work of Lumière and Couturier, however, was contradicted by that of numerous subsequent workers. In 1922 Kořínek (80) was unable to demonstrate antibodies resulting from the injection of saprophytic bacteria into plants. The same year marks the first of Carbone's studies in the field.

The following year negative results were obtained by Carbone (36) in potato inoculations, by Carbone and França (48) in feeding protein to insectivorous plants, and by Brown in connection with crown gall of paris daisy and rose (27). Cappelletti in the same year (29, 30) published the first of his studies dealing with acquired immunity in leguminose root tubercles. Carbone and Arnaudi in 1924 (45) were unable to demonstrate acquired antibodies in *Laurus*, although they made a notable contribution to the study of circulation of antibodies in plants. In 1925 Zoja (192), Hursch (75), Doussain (56), and Arnaudi (4) all reported successful vaccination of plants. Sardiña's results in 1926 (154) pointed to an absence of acquired immunity in a number of plant diseases, as did also those of Riker (152) with crown-gall.

In 1927 appeared the first edition of Nobécourt's excellent monograph upon the subject of acquired immunity in plants (136). He was able to vaccinate successfully, and came to the conclusion that although acquired immunity is present in plants it is customarily restricted to the cell and is not humoral in the sense of serology. Benigni in the same year (12) obtained a temporary immunity following vaccination of corn against smut.

Kostoff's long series of studies, in which numerous manifestations of acquired immunity were believed to result from grafting, tumor formation, hybridization, etc.,

began with a first paper in 1928 (82). The immunological interpretations of this work have been largely or entirely contradicted, however, by the work of Chester and Whitaker (52, 53, 187). Carbone in the same year published an excellent account of vaccination in plants (42) in which he inclined to the view that this phenomenon had been satisfactorily demonstrated. Likewise in 1928 Arnaudi (7) successfully vaccinated pea against *Blepharospora cambivora*.

The monograph in 1930 of Carbone and Arnaudi (47) supplied a working basis for more thorough investigation in this field and offered a comprehensive view of the work of these authors as well as of the numerous earlier investigators.

Finally several contributions of immunological significance have been reported in the past two or three years, of which the more important are East's observations on the recovery of sugar cane from the mosaic disease (60–62) and on the behavior of hybrid embryos in parent tissues (59, 60), Gravatt and Gill's hypothesis that an increased resistance of chestnut to *Endothia* canker may be due to acquired immunity (70), and the work of the school of Carbone furthering the study of antibodies in plants and emphasizing the necessity for distinguishing between true antibodies of the zoöimmunitary type and non-specific "pseudoantibodies."

This very brief chronological sketch having pointed out the main steps in the progress of the conception of acquired immunity in plants, we are now prepared for a more detailed discussion of the results obtained in this field. The following section will accordingly deal with the views, opinions, and *a priori* arguments regarding the possibility of acquired plant immunity, while subsequent sections will be concerned with the actual experimental data thus far obtained.

IV. A PRIORI ANALYSIS OF THE POSSIBILITY OF ACQUIRED IMMUNITY IN PLANTS

Although plants and animals are of presumably common origin they differ markedly in many gross structural and physiological properties. Are these gross differences such as to preclude the possibility of a display of immunological phenomena of the serological type? This is a question which in its various aspects has been considered by many of the investigators of plant immunology, and one which warrants the attention of the present section. The various points for consideration will be: (a) nature of the circulatory system, (b) manner of growth, (c) opportunity for sensitization, and (d) nature of disease and resistance to disease. These points will accordingly be successively considered.

Perhaps the most fundamental objection to an *a priori* belief that plants may elaborate antibodies is the difference of circulatory system between plants and animals in view of the fundamental rôle of the blood in elaborating and distributing immunological bodies. In the mammalian body we have an internal, relatively homogeneous current of high protein content and constant temperature rapidly pervading all parts of the body. An injected substance is soon distributed throughout the whole body and opportunity for sensitization is much more widespread than if the injected substance were localized at the point of original injection. The constant temperature and high protein content afford uniform and favorable conditions for antibody production and demonstration, conditions which certainly do not obtain in the plant body. For in the latter the conventional conception is of an ascending stream of water and mineral salts in the xylem system and a descending stream of elaborated food in aqueous solution in the phloem elements. The two systems are customarily

considered distinct, much less rapid than the blood flow, containing a much lower percentage of protein, and subject to much variation due to environmental variables. The conventional view does not ordinarily consider any appreciable horizontal transfer of elements from these streams nor reversal of flow. If this is the complete and accurate picture of circulation in the plant, then it would appear at first glance that the objections to the hypothesis of acquired antibody formation in the latter have some justification. Such objections, however, are based on three assumptions, namely that the blood stream is essential to antibody production and demonstration in animals, that immunization in animals is necessarily generalized throughout the animal body and not localized, and that the plant circulation differs from the animal circulation in the respects mentioned above. Recent investigations, however, have shown that none of these unreserved assumptions is justified.

That the mammalian blood stream is essential to the production of antibodies in animals has been contradicted by evidence from a number of sources. Thus the production of antibodies has been observed not only in vertebrates but also in many of the invertebrates, in which a blood stream is either lacking or of a type profoundly different from that of mammals. Moreover the studies of Carrel (cited in 173) and his associates have shown that it is possible to demonstrate immunological reactivity of isolated mammalian tissues in artificial culture entirely lacking a blood system. That immunization in animals is necessarily generalized throughout the animal body is refuted by the fact that certain parts of the body may be sensitized and may produce antibodies without this reactivity extending beyond the part inoculated. Thus Besredka (21) in an extended study of this subject shows, for example, that the skin alone of guinea pigs may be immunized to anthrax, that inoculation of *Staphylococcus* into the anterior chamber of the eye leads to immunity of the anterior chamber but of no other part of the body, and that ingestion of the dysentery bacillus by rabbit, mouse, or man is followed by a local immunity in the intestinal wall, the blood being unaffected. Finally the most recent investigations of the circulatory system in plants show it to be far less simple in operation than had been previously believed. Thus there is evidence that translocation in phloem and xylem is not restricted to motion down and up respectively but that reverse currents may occur, while lateral transportation is probably much more frequent than had been suspected. Transport may be relatively much more rapid than had before been believed. For example, East observed (60) in sugar cane that mosaic virus may travel as much as 18″ in 5–7 days. The possibility of circulation in the plant of precipitable animal protein has been demonstrated by Kraus, von Portheim, and Yamanouchi (96) who were able to recover in the plant the reactive constituents of blood serum in a solution of which the plants had been grown. Likewise Arnaudi (47) successfully employed serotherapeutic treatment in crown-gall of geranium by permitting the cut geranium stems to absorb animal antibodies, a process which is based upon the possibility of the circulation of antibodies within the plant organism.

There is very little doubt that it is possible for certain chemical substances at least to be so rapidly and effectively distributed throughout the plant as to function in prophylaxis. A. Müller in his extended treatise on the inner therapy of plants (131) records numerous instances of such effective distribution in the plant body. Wormald and Grubb (189) found that the substances responsible for immu-

nity of apple to crown-gall were circulated through the plant body and transmitted from immune scion to susceptible stock. This same was not true, however, in the case of immunity of potato against *Synchytrium endobioticum* (Roach, 153) nor in that of *Chrysanthemum* rust (Gibson, 68). There is, moreover, an extensive literature dealing with the translocation of various more or less complex chemical substances from one graft symbiont to the other. Evidence of such translocation of glucosides, alkaloids, and proteins is afforded by the experiments of Strasburger and Klinger (atropin), Laurent (atropin), Guignard (alkaloids, cyanohydric glucosides), Gräfe and Lensbauer (nicotin), Mitosch (albumin), Meyer and Timpe (factor controlling variegation), and Baur (virus). There are experiments in which the failure of certain substances to cross the graft union has been recorded, but for the purposes of our argument these positive results definitely indicate that the circulation of numerous complex organic substances including proteins is possible through the graft union, and the deduction necessarily follows that such complex substances are capable of effective circulation in the ungrafted plant.

It is possible to select for studying the circulation of antigenic material plants which are much more favorable than the ordinary flowering plants used. Certain algae and fungi which show rapid plasmatic circulation through large cells or long coenocytic stretches are particularly useful in this regard, *Phytophthora*, *Caulerpa*, *Nitella*, *Valonia*, and *Halocystis* representing a few such cryptogams. Almost nothing has been done in studying immunological reactions in such plants as these. To be sure Prát (142) reports a few experiments with *Caulerpa prolifera* in which he injected dyes and starch and then observed subsequent distribution of the injected substance. He found there was a limited distribution of the color but this was complicated by discoloration *in vivo*, by coagulation of the protoplast, and also doubtless by other traumatic effects since the dyes used (methylene blue, neutral red, Berliner Blau: leicht löslich . . . Grübler) although "vital" in the usual sense of the word undoubtedly exert some toxic effects after a period of observation as long as 2–4 days. In view of the inconclusive results of these experiments, *Caulerpa* and other similar plants could be investigated with profit, first as regards their circulation and proceeding from that to a study of their capability to acquire physiological immunity.

Hence we see that the *a priori* objections against the demonstration of acquired immunity in plants based upon differences in circulation are not as fundamental as first appeared, for not only can the animal show acquired antibody formation independent of the blood circulation, but also the circulation in plants is much more effective in distribution of antigenic material to the cells than had earlier been assumed.

A second difference between plants and animals leading to an *a priori* belief that the zoöimmunitary type of reactions could not play a practical rôle in plant pathology is that of manner of growth. The plant grows in an indeterminate fashion, continually producing new tissues from primary and secondary meristems, while the animal merely grows in size, the whole structure and form being determined from an early stage in development. Hence it might follow either that the plant would be incapable of any but a very transitory acquired immunity because the antibodies would be so diffused and diluted as to lose their importance, pathologically, or that a mechanism for the self perpetuation of the antibodies must be hypothesized.

This argument, it appears to me, is of somewhat greater importance than the

last, but it concerns primarily the practical applications rather than the theoretical demonstration of acquired immunity in plants. We are accustomed to think of acquired animal immunity in terms of long periods of time. Thus the period of protection from smallpox vaccination is customarily stated at seven years, that from typhoid vaccination at three years, etc. On the other hand we have very little evidence regarding the duration of acquired immunity in plants. The few experiments which have considered this point (12, 192) have indicated an acquired immunity in the plants employed of a duration of one to several weeks. This does not, however, preclude the possibility of a more extended period of acquired immunity. Even an acquired immunity of no longer than this serves to establish the theoretical possibility of acquired immunity in plants. Furthermore, a duration no longer than this might have important practical bearings as well, particularly in the cases of the diseases of plants in which the period of susceptibility is relatively limited ("damping-off" of seedlings, rust diseases, bacterial infections of succulent tissues).

Thus we see that the *a priori* argument against the demonstration and practical bearing of acquired immunity in plants based on the continuous, indeterminate growth of plants is interpreted in terms of an inactivation throughout progressive dilution of the immune substance which in turn would tend to limit narrowly the period of immunity. Such being the case, one sees from the foregoing analysis that this argument is of value only from the practical standpoint, not from the theoretical, and that also even from the practical considerations, granting that the activity of the plant meristems soon dilutes the antibodies beyond the point of their immunological functioning, yet in many important plant diseases the period of susceptibility is so short that the actual increase in tissues during this period could hardly be sufficient to exert any important diluting effect upon the immune bodies. It is thus unnecessary to hypothesize any mechanism of self propagation of the antibodies in plants in order to meet the argument set forth above.

A third point of comparison of plants and animals bearing on the *a priori* analysis of acquired immunity is that of the opportunities for sensitization in the two realms. The animal is subject to frequent local and blood infections which produce the effects we understand as immunological. Are plants different in this connection? On reviewing the subject of phytopathology one sees that the opportunities for sensitization are no less in plants than in animals, and perhaps greater. Beside the great number of bacterial and virus infections to which plants are subject, they also have many local and systemic fungus, algal, and vascular pathogens. They are likewise subject to toxic substances absorbed from the soil and inoculated by depredacious animals. That extracts from fungus, algal, and phaenogamous parasites may evoke specific antibody formation in animals has been demonstrated by the plant sero-diagnosticians, particularly Mez and his associates. Moreover the plant is not insensitive to the presence of foreign substances, in contrast to animals. Macht (107) has found plants to be highly sensitive to certain animal poisons, much more sensitive, in fact, than are animals to the same toxins. For example, the animal toxin cantharidin although only moderately toxic to animals is lethal to *Lupinus* in a dilution of 1:50,000. Accordingly we see from our *a priori* reasoning that there is abundant opportunity for plants to be sensitized by antigenic materials, that such antigenic materials evoke antibody forma-

tion in animals, and that plants show a sensitivity to the presence of foreign bodies commensurate with that of animals. The conditions present are thus favorable to the production of an acquired immunity in plants.

A last point to consider in our comparison of plant with animal reactions is the behavior of the two types of organism in disease. The animal reaction to disease is characterized by a number of clear-cut elements of the symptom complex. We recognize among these symptoms in animal disease a production of heat, an increase in protein, and a fluctuation of the pH. Such symptoms have also been demonstrated in plant disease, the production of heat by Richards (150) and Berlese (12a), the increase in protein in plant disease by Gioelli (69), and the fluctuation of pH by Wagner (180). Accordingly, from the evidence thus far available, one is led to agree with Quanjer (143) that there appears to be no fundamental physiological difference in the symptomatic reactions of plants and animals to disease. This affords no evidence but certainly does contribute to the prediction that reactions of the zoöimmunitary type might be anticipated in plants suffering from disease.

Briefly summarizing, then, we have seen that the *a priori* arguments against the demonstration of acquired immunity in plants based upon differences in circulation, in manner of growth, in sensitivity to foreign bodies, and in reaction to disease are in no case valid objections to the thesis. We have seen, on the contrary, that there is a certain amount of evidence tending definitely toward an *a priori* belief in this capability in plants. Among the chief exponents of the *a priori* argument against this capability in plants are Blackman (22, 23) and Leach (101). Other students such as Walker (182) and Sorauer (164) have analyzed the field of plant immunity without at all considering the possibility of acquired physiological immunity in plants. On the other hand, we have a considerable number of investigators who have considered the theoretical possibility of this phenomenon in plants and who are inclined to favor this possibility. Among the latter may be mentioned Ward (183, 184), Bolley (25), Vavilov (176), and Gäumann (66) with particular reference to the immunity of grains to *Puccinia* species, Brierley (26) and East (61) regarding the recovery of plants from virus diseases, Steiner (167) concerning immunity of plants to nematode infestations, and numerous others (174, 128, 129, 159, 81, 173, 120). Carbone in his earliest studies (35) was somewhat pessimistic as to this thesis, but in later works (36, 42, 43, 44) he has taken a definitely favorable view of it. The reader interested in these theoretical considerations regarding acquired immunity in plants is recommended particularly to the works of Carbone and Arnaudi (47), East (60), Blackman (22, 23), Silberschmidt (159–161), Gäumann (66), Doussain (56), de Tomasi (174), Kořínek (81), Moritz (125, 126), and Tobler (173).

V. NORMAL ANTIBODIES IN PLANTS

In determining the presence and nature of acquired antibodies in plants it is first necessary to have an understanding of substances normally present in the unsensitized plant which exert an antibody effect upon foreign bodies. Such normal precipitating, agglutinating, or dissolving substances are here referred to as *normal antibodies*. The purposes of investigating them are twofold, first because normal antibodies occur in animal blood subject to the same laws as those governing acquired antibodies, and accordingly represent not only an important part of the mechanism of immunity but a mechanism homologous

in physico-chemical behavior with that of acquired immunity, the normal reactions thereby shedding light upon the acquired reactions; and second because in all antigen-antibody experiments control tests involving the normal reactions must be performed, and only by the understanding and elimination of these normal reactions can the acquired reactions be considered significant, i.e., truly acquired.

In order to systematize the present and subsequent discussions the subject matter will be classified primarily according to the type of reaction, whether agglutinin reaction, lytic reaction, etc., and secondarily according to the host-antigen groups. No attempt will be made to follow a rigid chronological order, since the subject content is much more clearly understood by grouping as indicated. It must be mentioned that from what we know of animal serology there is strong evidence that all of the protein reactions (agglutination, precipitation, lysis) may be due to a single type of antibody, reacting differently according to the physical form of the antigen, in which case our arrangement may be somewhat unnatural and arbitrary. However, in view of our lack of complete information on this head the present system is considered most suitable for the elucidation of the thesis. Proceeding, then, according to this scheme, we will first consider the normal agglutinins in plants, then the normal lysins, pseudolysins, antilysins, etc., next the normal precipitins, and finally other types of normal antibodies in plants.

A. Normal agglutinins in plants

As early as 1902 plant products had been tested against blood corpuscles for the determination of the presence of normal agglutinins in such products. Kobert in this year (79) tested certain plant protein solutions (ricin, abrin, crotin, and robin) against the bloods of various vertebrates including mammals, birds, amphibia, and fish, and found in many cases that these protein solutions agglutinated the blood corpuscles in very high dilution (up to 1:600,000). Extracts of bacteria also exerted an agglutinating action on such corpuscles, an indication of the wide range and probable primitiveness of the normal agglutinin reaction. The same year Kraus (95) performed similar experiments with the reactions of abrin and ricin against mammalian blood with entirely comparable results. Extracts of leguminose seeds were tested against a similar variety of bloods (mammal, bird, amphibian, fish) by Landsteiner and Raubitschek in 1907 (100). Normal agglutinins were found to be present in various cases and highly potent (reactive in dilutions of from 1:400 to 1:32,000). These were not precipitated by acid, were destroyed by boiling, were precipitated by alcohol and ammonium sulphate, and were dialyzed with difficulty. Hence they were probably protein in nature. The experiments with ricin were again repeated and confirmed by von Eisler and von Portheim in 1909 (63). This type of work was continued by Schneider in 1912 (156), who also found a very active haemagglutinating agent in bean proteose and other bean proteins. This active principle gradually disappeared from the cotyledons simultaneously with the stored food as the seedlings developed and it was not present in other parts of the plant. In the same year rice extract (Kanahara, 78) and in 1913 corn extract (Liu and Bacelli, 103) were found to contain normal haemagglutinins.

Extracts of potato tubers were found to possess haemagglutinins by Vigliano in 1922 (178), by Marcusson-Begun in 1926 (119), and by Carbone and Arnaudi in 1930 (47), while they also showed bacterio-agglutinins according to Wagner in 1915

and 1916 (179, 180) and Berridge in 1929 (20). The properties of these potato agglutinins were investigated by the various workers with interesting results. Marcusson-Begun (l.c.) found the haemagglutinins to be active in a dilution of from 1:20 to 1:50,000, weakened by heating to 60°C., destroyed by boiling (contradicted by Vigliano's findings in 1922), adsorbed by susceptible corpuscles, and later freed by warming. The bacterioagglutinins according to Wagner (l.c.) were destroyed by two hours heating at 45°C., were precipitated by $(NH_4)_2SO_4$ but again recovered in active form in the washed and redissolved precipitate, and disappeared with the approaching death of the tubers. Miss Berridge found the agglutinating power to be due to substances precipitable by 95 per cent alcohol and subsequently soluble in water, and also observed a very interesting relationship between pH of the potato sap and the agglutinin reaction, in that the agglutinating power of the potato precipitate for any one species of bacterium varied with the pH of the solution, the species differing among themselves in the respect that potato-pathogenic bacteria were not agglutinated at the normal pH of the sap while potato-innocuous bacteria were agglutinated at this pH, a condition perhaps of importance in the normal immunity or susceptibility of the potato against various bacterial species. She suggested that the agglutinative power may be due to traces of salts of di- and trivalent metals.

Agglutinins have also been found in extracts of certain of the fleshy fungi, in particular haemagglutinins in *Boletus* (Carbone and Arnaudi in 1930, 47) and bacterioagglutinins as well as haemagglutinins in *Armillaria mellea* (Vigliano 1922, 178). The latter were not destroyed by boiling. Carbone in 1904 (47), however, found no haemagglutinins in *Armillaria mellea*.

Passing now to the studies of normal agglutinins in the vegetative tissues of the higher plants, we have an abundance of data available. Normal haemagglutinins have been found in *Datura* by von Eisler and von Portheim (63) in 1909, although very extensive tests in ninety-eight other species of fifty-five genera failed to reveal such principles. A few years later Kritschewski (97, 98), found bacterioagglutinins in *Cotyledon Scheideckeri* potent at a dilution of 1:150 to 1:500, somewhat variable but present in the different parts of the plant, and apparently an inclusion of the cell sap. These were highly thermostable (to 134°–144°C.), were not subject to proteolytic digestion by pepsin and trypsin, were lost on standing 3–4 days at 37°C. and partly lost by standing at 5°–7°, and were dialyzable only in part. The active sap gave no protein reactions, the active principles were not adsorbed or inactivated by animal serum, they were capable of being so strongly bound to the antigen that neither 75°C. nor acids were able to dissociate the bond, and they were wholly held back by a Chamberland filter. He believed that the normal antibodies for the various bacteria were identical.

Beside his experiments with potato tubers mentioned above, Wagner in 1915 and 1916 (179, 180) also tested *Sempervivum* and *Beta* finding bacterioagglutinins also present in these plants, possessing the same properties as enumerated above (presumably protein). In 1922 (178) Vigliano tested a number of other plants and found bacterioagglutinins in citrus fruits, onion tubers, *Stachys* roots,. carrots, cabbage, spinach, celery, salsify, and *Opuntia*, and haemoagglutinins in citrus fruits, endive, spinach, chicory, cabbage, egg-plant, cauliflower, and onions. The degree of bacterioagglutination differed in the same plant for the different species of bacteria.

The agglutinating principle in endive was filterable through asbestos.

Kořínek reports experiments in 1924 (81) with *Beta* (root extract) and *Euphorbia* (latex) in which were observed normal "agglutinins" for *Bacterium tumefaciens* in only the former species. These "agglutinins," however, were believed by the author to be entirely different from serological agglutinins, presumably acting through a simple chemotactic mechanism. The same year Carbone (37) furthered the conception of false agglutinins or to use Carbone's term "pseudoagglutinins." Such pseudoagglutinins he found in *Prunus laurocerasus* leaf extracts, the principles being particularly active against typhus bacteria, rather thermostable although destroyed by boiling, passing easily through filter paper but poorly through filter candles and not at all through asbestos, and being independent of the pH or age of the leaves. Carbone and Arnaudi then furthered their researches in this direction using *Morus* and *Salix* (45, 46). They found in the rising sap of the mulberry a haemoagglutinating and bacterioagglutinating substance and in the willow a bacterioagglutinin. These substances, however, were not always positive to all the antigenic species and varied somewhat from plant to plant. They were again relegated to the category of pseudoantibodies. Riker failed to find any normal agglutinins toward *Bacterium tumefaciens* in his researches in 1926 (152).

B. *Normal lysins in plants*

Passing next to the subject of normal lysins in plants, reserving analysis and discussion of all these normal reactions until a complete statement of the evidence available is before us, we find that experiments regarding lysins in plants are as abundant as those concerning agglutinins. In fact, since both agglutinin and lysin reactions are observable with the same technique and preparations, observations of the two reaction types have customarily been made by the same worker at the same time.

Kobert again paved the way in 1902 (79) for a study of normal plant lysins in showing that crotin dissolved corpuscles of rabbit and crow. In 1909 von Eisler and von Portheim in their many tests of plant extracts against blood of various vertebrates (63) found haemolysis to occur only with *Salpiglossis* extract. The following year Wilenko (188) using the complement-fixation technique, a refinement of the simpler procedure in the study of lytic reactions, observed that ricin, abrin, bean-protein, crotin, corn protein, and oat protein generally reacted against a variety of mammalian, bird, and fish bloods. The reactive substances were relatively thermostable. Wagner, whose studies with agglutination have already been mentioned, also reported in 1915 and 1916 (179, 180) positive bacteriolysis tests with potato, *Sempervivum*, and *Beta*. Here the antibody behaved just as the agglutinins in being thermolabile and precipitable but recoverable by $(NH_4)_2SO_4$. Likewise Vigliano in 1922 (178) found normal hemolysins in *Armillaria mellea* which were coctostable. In 1924 and 1925 Carbone and Arnaudi (5, 45, 46) suggested that the hemolysins found by them in mulberry were not true antibodies ("pseudo-deutero-hemolysins"). They were found in the rising sap, appeared thermostable *in vivo* but were certainly thermolabile *in vitro*, and acted particularly against sheep corpuscles but only in the presence of *fresh* rabbit serum. Arnaudi believed them to be a product of the living cells of the wood vessels. Although perhaps not strictly a lytic reaction one may recall at this point that Miss Berridge's work with potato extracts included plasmolytic reactions subject to the same comments as her agglutination reactions and probably due, she believed, to the

presence of phosphates in the potato extract. Carbone in 1904 (reported in 1930, 47) had noted an inconstant hemolytic power in *Armillaria mellea* and a hemolytic action in *Boletus* species. No normal lysins against *Bacterium tumefaciens* were found by Riker in 1926 (152).

In a series of publications commencing in 1928 Kostoff has described normal proteolysis in solanaceous extracts, demonstrated by ring testing (82, 84) and by the ninhydrin-dialysis reaction (88, 90, 91). Similar lytic rings were observed by the writer in 1931 (50) between certain oleaceous extracts, but at that time little significance was attached to them. Subsequent investigation (53) has shown the "lytic rings" to be entirely aspecific and independent of protein, occurring between extracts and certain salt solutions. Kostoff's ninhydrin-dialysis tests, on the other hand, have not yet been confirmed by other workers.

Beside lysins, antilysins, substances which inhibit the activity of lysins, have been found in normal plants. Vigliano in 1922 (178) found anti-hemolytic substances in citrus fruits, endive leaves, *Opuntia* cladodes, *Stachys* roots, and potato tubers. The active principle in the potato he found to be coctostable but inhibited by low temperatures (13°–15°C.), while it was not filterable through asbestos. The mulberry extract investigated by Carbone and Arnaudi (45, 46, 5) which was normally haemoagglutinative became anti-haemoagglutinative in the presence of certain fresh or inactivated sera. Anti-haemolysins were also found by these workers in *Prunus laurocerasus*. Arnaudi (47) also confirmed Vigliano in finding anti-haemolysins in potato tuber extract.

C. *Normal precipitins in plants*

Passing next to the normal precipitins of plants we again find a wealth of experimental data available, but unfortunately much of it undoubtedly involves reactions of the "pseudo" type. The first record of the presence of precipitins in plant products was that of Kraus in 1902 (95) in which he reported a sero-precipitating action of ricin solutions on rabbit blood (not on goat blood) but absence of this action in abrin solutions. In 1907 Landsteiner and Raubitschek (100) found that bean extract precipitates hen and horse sera. Three years later Wilenko (188) using ricin, abrin, bean protein, crotin, corn protein, and oat protein observed that these generally precipitated a variety of vertebrate blood sera. The precipitating power of the *plant albumens* was lost on heating them to 80°C., although the reactivity of the *sera* was not destroyed on heating to high temperatures. Moreover an excess of serum caused a decrease of precipitin reactivity. Schneider in 1912 (156), Kanahara in 1912 (78), and Liu and Bacelli in 1913 (103) demonstrated precipitins in bean, rice, and corn extracts respectively. Precipitins of extracts of bacteria and of horse and frog serum were found by Kritschewski in extracts of *Cotyledon* and of seed albumen in 1914 and 1915 (97, 98). These were active in dilutions of 1:150 to 1:200, were present apparently in the cell sap of various parts of the plant, were highly thermostable (even to 144°C.), were insensitive to proteolytic digestion, were imperfectly dialyzable, and were held back by the Chamberland filter "F." The precipitins present in *Cotyledon* were apparently identical with the agglutinins present. The plant extract used contained no demonstrable protein and it produced precipitation of human urine which also contains no chemically demonstrable protein. Precipitin and antigen in this case showed a high affinity which was not dissociated either by 75°C. or by the presence of acids. Vigliano's studies in 1922 (178) also included the finding of normal serum precipitins in citrus fruits (due to

acidity), *Opuntia*, celery leaves, and onion bulbs.

Kostoff's interest in 1928 and subsequently (82, 84, 85, 86, etc.) was primarily concerned with the precipitin reactions in solanaceous extracts. These were tested both by direct readings of the ring test and by nephelometer readings. He found normal precipitins, so-called, in many of his combinations of extracts. These "normal precipitins" were subsequently investigated by Silberschmidt who carefully analyzed the reaction techniques from the standpoint of protein reactions (161). However, Chester and Whitaker (52, 53) in an extended study of the nature of these "antibodies" found that a large percentage of the reactions called "precipitin reactions" by Kostoff and Silberschmidt were in reality simple precipitations of calcium oxalate. Four types of reaction were obtained by these workers in the thousands of tests performed. Of these four reactions the main one was the calcium oxalate reaction just mentioned. A second precipitation type (AB) was distinguished in which the reactive principles were likewise plainly non-protein and non-lipoid but organic and of relatively high molecular weight. A third reaction (MN) was the result of the interaction of two organic substances one of relatively simple structure and presumably non-protein, the other probably protein. The fourth reaction identified (XY) was so weak and infrequent as to render analyses impractical at the time of experimentation. Kostoff's, Silberschmidt's and Chester's earlier "precipitin reactions" were all found to be interpretable according to the analysis of Chester and Whitaker, which analysis now affords a suitable basis for further investigation. That most of the "precipitin reactions" reported by these workers are non-immunological, due to "pseudoantibodies" in the broad sense of the term, has been rendered evident. That some, notably the MN reaction, may possibly be of the type of serological reactions is not denied, however, even though only one component appears to be protein in nature. East has also performed a few precipitin tests of normal extracts of various species of plants including sugar cane (61). In some cases he obtained positive results. That these positive reactions are susceptible to the same sort of explanation as those of Kostoff, Silberschmidt, and Chester is presumable, although the tests of the particular species employed by East were not included in the analysis of Chester and Whitaker.

D. Other types of normal antibody reactions in plants

Our concepts and terminology of immunological reactions in plants have been largely borrowed from the serological literature. In serology the antigen is either a discrete microscopic particle (bacterium, corpuscle) or a solution usually or always of protein. The antibodies are contained in a solution (serum, tissue extract). The possible reactions are clearly distinguished as agglutination, lysis, precipitation, etc. *in vitro*, and anaphylaxis, amelioration of symptoms, or recovery, etc. *in vivo*. Plants, however, could not inconceivably display additional types of reaction. For example, the attacks of fungi on plants depend upon spore germination and penetration, mycelium- and haustorium-formation, and sporulation. Apart from the dermatomycoses, a relatively insignificant group of human diseases, there is little or no counterpart in animals to the fungus diseases of plants. This being so we must look for possible immune reactions in plants distinct from those of serology and appropriate to the peculiarities of plant sensitization and disease. A very few illustrations of such reactions in nor-

mal plants have been reported, although, as will be seen later, there is a somewhat greater number of such acquired reactions which have been observed.

In his studies in potato, *Sempervivum*, and *Beta*, Wagner in 1915 and 1916 (179, 180) described normal immune bodies which check the motility of the cilia of certain bacteria. These are analogous and perhaps homologous with the normal agglutinins described by other workers but find their expression in a reaction entirely distinct from ordinary bacterioagglutination. Moreover he also found present in these plants substances which prevent the germination of bacterial spores and of bacteria protected by thick membranes.

Carrying this type of reasoning over to the field of fungi we find a great many experiments which have been reported regarding substances in plants which inhibit growth of fungus mycelium and their relationship to immunity and susceptibility of the plants in question to the respective fungi. No attempt will be made in the present instance to review this work in detail but a few instances will be given to illustrate this point. Ezekiel, Taubenhaus, and Fudge in 1932 (63a) found that the growth of *Phymototrichum omnivorum*, a fungus causing root rot, was markedly inhibited in the undiluted although autoclaved juices from all of the resistant plants used, while profuse and heavy growth was obtained in juices from three of the four susceptible plants employed. Similarly extracts of red and yellow onions contain substances inimical to the onion smudge fungus, growth of *Fusarium lini* is partially inhibited by extracts from resistant species of flax, and some citrus bark extracts have a detrimental effect upon certain bark disease fungi. Comparable results have been obtained with corn extracts and *Ustilago zeae* and with wheat extracts and *Puccinia graminis*. For a review of the results in this field and for references to the recent literature dealing with it the reader is referred to the work of Ezekiel, Taubenhaus, and Fudge (l.c.).

In all these cases, however, there is grave question whether the inhibitory effects are due to antibodies in the zoöimmunitary sense or to relatively simple, non-immunological chemical substances present in the extracts. The presence of toxins, of unfavorable pH relationships, the lack of suitable nutrients, all these and many other non-immunological factors undoubtedly come into play in such growth inhibitions, and thus far little of the work in this field has contained definite conclusions as to the precise nature of the inhibitory substances. We must hence view such work very cautiously, reserving definite immunological conclusions till more thorough analysis is available.

E. Analysis of the foregoing data

With the data regarding normal immunological reactions of plants before us we are now in a position to evaluate these data from the immunological standpoint. Many positive results have been obtained regarding normal agglutinins, precipitins, lysins, and growth-preventive substances. To what extent are these reactions immunological in the zoöimmunitary sense, what is their relationship to acquired immunological reactions in plants, and what is their practical rôle in phytoimmunology? These are the questions which will be considered in the present section.

Regarding the nature of these plant reactions we are first required briefly to review the nature of animal antibodies and then to compare the two. Although few points regarding the animal antibodies may be stated as absolute principles, yet they have certain outstanding characteristics which are at least their usual properties. In the first place, it is generally held, al-

though not absolutely proven, that animal antibodies are proteins. The possibility of immunological reactivity seems to depend upon the large molecular size of the protein molecule, although the specificity of the reaction may depend upon relatively small radicals of the molecule. The animal antibodies are usually relatively highly thermolabile, presumably because of the coagulation of protein at the higher temperatures. Similarly they are affected by the usual protein treatments (precipitated by alcohol and $(NH_4)_2SO_4$, retained by dialyzing membranes, their solution and reactivity correlated with the presence of electrolytes, behavior as colloids). The agglutinins and precipitins are inhibited by an excess of either antibody or antigen (zone phenomenon), are readily attacked by pepsin, less so by trypsin, are destroyed by alkalies, less so by acids, and are adsorbed by suspensions such as animal charcoal. The lytic reactions are possible only through the activity of two components, one, the immune body (amboceptor), which may be identical with the agglutinins and precipitins, the other, the complement, which is present in normal serum, is non-specific, is apparently composed of two protein components, and is highly thermostable and inactive to other physical and chemical agents. With this very brief résumé of the properties of animal antibodies we may now turn to the normal reactive substances in plants.

It is necessary to use some standard for comparison between animal and plant antibodies. Such a standard, it appears from our present knowledge, is best of the following form. Plant antibodies should give evidence of protein nature, they should if acquired show specificity directed toward the antigen employed, and they should be active in relatively high dilution. How do the plant phenomena described above conform to this standard? Unfortunately many of the students of the normal antibodies have not investigated their nature and properties, and accordingly much of the evidence now available is insufficiently complete for accurate evaluation.

As regards the agglutinins we know that certain protein solutions may show a very potent agglutinating effect, comparable in delicacy to the blood reactions (see the work of Kobert and others above). It thus seems evident that the experiments performed with ricin, crotin, abrin, etc., point definitely to a homology between the normal agglutinative property of these proteins and that of mammalian blood. The agglutinins of potato are highly potent but it appears that there are at least two agglutinative principles present in potato, one of the true antibody type (Marcusson-Begun, 119) and one relatively simpler, probably non-protein, and of the "pseudoantibody" type (Arnaudi, Berridge). The reaction of plant antibodies or pseudoantibodies to heat, a most important character in serology, is not as accurate a criterion as might be desired, because of the much greater resistance of plant proteins to heat (138a). Kritschewski's "bacterioagglutinins" in *Cotyledon* (97, 98) can hardly be considered true antibodies, since they give none of the customary reactions of proteins. This same applies to the findings of Kořínek (81) and Carbone (37). The other "agglutinins" reported have not been sufficiently investigated to warrant their recognition as either true antibodies or pseudo types. We may thus conclude that so far as data are available true normal agglutinins of the serological type are present in some plant preparations but that there are also present non-protein agglutinative principles which must be carefully distinguished from the former in all critical work.

We have only one instance of normal

lytic reactions in plants which without much question is of the serological type, that of Wagner in 1915 and 1916 (179, 180). Here the active principle is plainly in the protein fraction. All other cases thus far reported, with the possible exception of Kostoff's dialysis-Ninhydrin experiments, are either clearly of the "pseudo" type (the results of Carbone and Arnaudi in particular) or are insufficiently described for accurate conclusions. Kostoff's "lytic rings" are plainly due to non-protein components, but his dialysis experiments, if confirmed, would offer valuable evidence as to the presence of true lysins in plants. Likewise the antilysins are but poorly understood. The fact that they are not filterable through asbestos, indicating that they are either of great molecular size or are adsorbed, would seem to indicate that they are protein, and if so it is presumable that they may also be of the true immunological type.

The precipitations of Wilenko's protein solutions (188) seem to be clearly of the immunological type according to our standard both in their thermolability and in their simulation or duplication of the zone phenomenon. Those of Kritschewski (97, 98) are presumably not of the true antibody type, their potency being weak (only to 1:200) in comparison with animal precipitins, and their very great insensitivity to heat arguing against their true antibody nature. On the other hand they are either of great molecular size or are adsorbed to large particles of the tissue pulp, a situation clearly suggesting proteins, yet no chemically demonstrable protein was present in Kritschewski's preparations. It is not beyond possibility that chemically demonstrable protein and immunologically active protein are distinct. Our chemical tests for protein in practically all cases are tests not for the protein nucleus of the molecule but for certain relatively insignificant radicals of such molecules, and accordingly one must not feel that absence of chemically demonstrable protein is a positive proof of the absence of serological protein. However in view of the fact that most proteins are chemically demonstrable, one may reasonably assume the probability that the precipitating extract containing no demonstrable protein by chemical tests is of the pseudo type, and that applies clearly to Kritschewski's "precipitins." The "normal precipitins" of Kostoff and Silberschmidt are certainly in most cases and perhaps all, according to the analysis of Chester and Whitaker, "pseudoprecipitins," non-protein and not homologous with animal precipitins. We thus have only the results of Wilenko pointing to the presence of normal precipitins of the serological type, we have numerous findings indicating the presence in plants of "pseudo-precipitins," and we have a quantity of data at present unanalyzable because the nature of the "antibodies" reported was not investigated.

The growth-inhibiting substances, the last of the groups of normal antibodies described above, have in no case been analyzed for their true nature. Only conjecture is permissible regarding their homology with animal antibodies, but it seems reasonable to assume that in many such cases if not in all these substances are in the same category as the pseudoantibodies described above.

We thus see that there is clear-cut evidence in the data at hand showing the very frequent presence in plant extracts of "pseudoantibodies," substances of non-protein and in some cases probably very simple structure, which through non-immunological processes produce the agglutination, precipitation, and lysis of foreign bodies. In addition there are a few cases in which the presence of normal agglutinins, precipitins, and lysins of the

zoöimmunitary type appears to be demonstrated to satisfaction. More of these should be investigated. Their nature and relationship to acquired phenomena should be better understood. The evidence presented shows that the investigation in this direction has yielded worth-while results and has opened a new field of study. We are warned of the occurrence and something of the nature of the "pseudo-antibodies" and the way is accordingly clear for a careful, critical investigation of the rôle of these two types of phenomena in plants. Moreover, the pseudoantibodies should not be rejected theoretically because of their heterology with animal antibodies. It may be that these have an important, although non-specific rôle in internal prophylaxis. The work with growth-inhibiting substances cited above certainly indicates such. And finally both as regards the true normal antibodies in plants and the pseudoantibodies, an understanding of their nature must ultimately lead to a thorough study of their function in plant disease, wherein lies the crux of the whole problem before us.

VI. ACQUIRED IMMUNITY FROM TREATMENT WITH ANTIGENIC SUBSTANCES

In the preceding section we have considered the normal antibodies in plants. With this section affording a background we are now able to proceed to the more vital subject of acquired immunity in plants. Acquired immunity may result from various manifestations of the same cause, namely the introduction into the plant of stimulative or antigenic material such as proteins or toxins. The nature of the antigen and the method of introduction serve to differentiate the various manifestations shown by the plant. In simplest form the stimulative substance may be merely injected or absorbed through the roots. Its composition is determinate, its toxic effects may be studied in a relatively simple condition, and thus the *principles* of acquired immunity may be investigated. In *practice*, in nature, the process of sensitization is somewhat more complex. Thus in a bacterial disease of a plant the reaction of the plant may be toward the whole organism (agglutination, lysis) or toward its enzymes or excreted substances, or toward the plant's own altered components (disintegration products), or toward any combination of these. Moreover, in parasitism we do not have the simple stimulation of a single injected substance, but we have many foreign substances toward which a plant is reactive which is for various reasons abnormal in its behavior, chiefly because of morbid or neoplastic reactions to parasitism. Symbiosis is a further aspect of parasitism and subject to similar modifications of the simple antigen-antibody relationships. We shall accordingly first consider the simpler situation, namely the sensitization by introduced substances of determinate composition, and then proceed to the more complex manifestations of acquired immunity in parasitism, symbiosis, and hybridization.

As was stated on a preceding page, the term antigen is customarily delimited to refer to foreign substances of protein nature which induce the formation of specific antibodies. However, this term in a broader sense includes certain non-protein toxins which induce in the plant a toleration or antitoxic reaction in many respects comparable to the usual antigen-antibody reactions and accordingly a discussion such as the present one would be incomplete without some reference to such antitoxic reactions in plants. This having been considered we may pass to the next simplest condition, namely the reactions of the plant to the introduction of protein in solution (unformed antigenic material) and

finally to the reactions of the plant to the injection of corpuscular antigens (formed antigenic material). The present section will accordingly treat in turn of these three aspects of the problem of acquired immunity to artificially introduced antigenic material.

A. Artificial introduction of non-proteins

There have been very few studies of the acquirement of immunity by plants toward non-protein stimulants. Of these, however, certain ones are deserving of mention. The Corn-cockle, *Agrostemma githago* elaborates a saponin which is highly toxic to both plants and animals. In 1918 Combes (54) cultivated various species of plants under aseptic conditions in Knop's solution to which had been added this saponin in concentrations of 1:10,000, 1:4000, 1:2000, 1:1000, 1:500, and 1:100. With all plants and in all dilutions the saponin acted as a noxious substance to the roots of the plants which did not produce this poison, while it had no toxic effect even in the strongest concentrations upon the roots of *Agrostemma githago*. Combes therefore concluded that the superficial cells of the roots of *A. githago* are immune to the saponin which this plant elaborates and accumulates in its seeds. Whether this immunity is hereditary or acquired in the strict sense of the word is somewhat questionable, but it deserves attention in the light of the apparent antitoxic effect displayed.

In 1925 Richet, Bachrach, and Cardot observed a very striking reaction of bacteria toward toxins in the nutrient substrate (151). Employing a bacterium which ferments lactic acid these workers grew the organism for several months in nutrient solutions containing thallium nitrate in varying concentrations. Then all the cultures were transferred to a medium containing .2 per cent of the salt. Their reactivity was then measured by observing their relative abilities to ferment lactic acid. Using the fermentation of the non-sensitized bacteria as a standard, these workers found that the cultures sensitized with .001 per cent and .01 per cent of the salt showed a decreased reactivity, which was interpreted as an anaphylactic reaction, while the cultures treated with .1 per cent of the salt showed a gain in reactivity over the controls of 50 per cent, a phenomenon believed to represent increased toleration or mithridatism. It is very difficult to compare with the reactions of macroscopic animals and plants those of bacteria, the individual existence of which is so ephemeral. However, considering the cultures *in toto* these results are most interesting, for not only do they yield evidence regarding acquirement of immunity (exhibited in two fashions) in a plant, but they afford evidence of such immunity in one of the simplest of all organisms, a situation pointing to the primitiveness and fundamental nature of acquired immunity. It is to be hoped that these studies of Richet and his colleagues may be further substantiated.

Carbone (37, 47) has mentioned a very brief work by Santori in 1925 (153a) in which it was claimed that plants are able to form substances neutralizing strychnine and various other toxins when the latter have been absorbed. I have been unable to find this work of Santori's and Carbone makes no further comment upon it.

Finally Leemann's work in 1932 contributes somewhat toward our knowledge in this field, although it is rather difficult to interpret his results with clearness. Leemann treated wheat seedlings in soil with various types of extracts and observed their subsequent degree of susceptibility toward *Helminthosporium sativum* (102). Certain solutions such as water extracts of *H. sativum*, bacterial decoctions and fractions

thereof, and lipase increased the resistance of the seedlings, while other solutions such as certain other bacterial decoctions, diphtheria toxin, and olive oil+lipase increased the susceptibility of the plants. This work, which suggests a non-specific antitoxic effect in some instances, is not wholly clear, not only because of the complexity and indeterminate composition of some of the introduced substances, but also because of the probable variability of the genetic constitution of the seedlings, the composition of the soil, and other possible uncontrolled factors.

We thus see that the evidence regarding antitoxic effects in plants is very limited. All, however, points in the same direction, and it thus seems probable that under some conditions at least plants can either acquire a tolerance to or actively combat foreign non-antigenic toxic material by reactions of the type of antitoxic reactions in animals. Leemann has pointed out (l.c.) the very important practical considerations arising from such a situation, and hence both from the theoretical and the practical viewpoints this subject represents a field in which a few carefully controlled experiments would be highly desirable.

B. Artificial introduction of soluble proteins

A somewhat greater amount of evidence has accumulated regarding the behavior of plants following sensitization with soluble proteins as antigens. Such behavior may take one of several forms of which anaphylaxis and precipitin reaction have been investigated in particular. Chronologically the first of these studies was that of Lumière and Couturier in 1921 (105, 106). Using *Rumex* and hyacinth leaves and onion bulbs these workers injected the tissues with varying small doses of horse and ass serum. After intervals of 30, 21, or 15 days a second dose of serum was administered with the result that the sensitized plants completely withered and died after 4–8 days, while the controls which had received only one dose (either first or second) remained healthy. The death of the sensitized plants was attributed to anaphylactic shock. Here appears to lie a clear-cut case of anaphylaxis in plants, yet these results of Lumière and Couturier have been carefully repeated in detail and with variations by Longo and Cesaris-Demel (104), Nobécourt (135), Otto and Herrig (139), Novoa-Santos and Criado (137), and Carbone (38), none of whom were able to observe any reactions attributable to anaphylaxis. Beside sera of various sorts, leucosin, a plant protein, was used for sensitization by Longo and Cesaris-Demel; beside Lumière and Couturier's plants this phenomenon was tested on *Lilium, Clivia, Impatiens, Lupinus, Begonia, Sambucus* and several other species of plants by Longo and Cesaris-Demel, on *Vicia* by Nobécourt, on *Lilium, Clybia, Xantedeschia,* and *Mimosa* by Novoa-Santos and Criado, on *Sedum, Echeveria, Sempervivum, Bryophyllum, Mesembryanthemum,* and *Kalanchoe* by Otto and Herrig, and on potato by Carbone. The work of these last investigators was careful and thorough, at least as much so as that of Lumière and Couturier, and some of the additional plants investigated (*Mimosa* in particular) would appear to be admirably adapted to this type of work. We are hence forced to conclude with Nobécourt that either the plants of Lumière and Couturier died from infection, or that anaphylaxis in plants is dependent upon processes yet unknown. It is of course self-evident that with such delicate reactions as anaphylaxis a single negative result is not very significant, because anaphylaxis is manifested only when the two doses are very accurately measured and spaced and when the experimental organism is sensitive to the foreign protein. However the various repetitions of this work

tend to make one rather skeptical of the results of Lumière and Couturier, particularly as one examines their figures of the "shocked" plants in which as Nobécourt points out the "plantes complètement pourrie" resemble plants killed by bacteria or *Botrytis*.

However, the view that anaphylactic shock may occur in plants, and indeed in very primitive ones, is not without some further substantiation. In 1922 Arloing and Thévenot (3) obtained positive results using as experimental organisms bacteria of several species. The serum used for sensitization was mixed with the bouillon in which the cultures were growing, a stronger dose of serum was added for the second treatment, and subsequent behavior was observed on ordinary agar. Modifications of the vegetative growth, pigment-producing power, and virulence were observed in the treated cultures, the growth in particular of the "anaphylactic" cultures being markedly inhibited.

If this work of Arloing and Thévenot is sound then not only have we another positive record of anaphylaxis in plants but we also have a further record of acquired physiological immunity in bacteria, of great interest in connection with that mentioned above of Richet and his colleagues concerning antitoxin formation and anaphylaxis in bacteria. Whatever the nature of this reaction in bacteria called anaphylaxis it has been twice recorded by two sets of observers, and it certainly suggests anaphylaxis in animals. With organisms as numerous and prolific as bacteria in a colony, it is probable that natural selection may play a far greater rôle in a short time than in the larger, multicellular experimental organisms. Such might account for the habituation of a colony of bacteria to increasing doses of a noxious substance. But in the present connection the phenomenon investigated is not toleration although it may possibly be correlated to it (power of fermentation in the first case, growth on ordinary agar in the second), and it hence appears either that there is some phenomenon in bacterial physiology simulating anaphylaxis or that anaphylaxis actually does occur in these lowly organisms and that it may impress itself upon the progeny of the "shocked" individuals. An answer to this problem is not possible at the present time, but it would be of great interest from the various standpoints of plant and animal immunity, of genetics, and of bacteriology.

Beside observations regarding anaphylaxis in sensitized plants, the only other work mentioned in the literature is that of Carbone and Arnaudi (46). These workers in their experiments with *Prunus laurocerasus* and *Morus alba* attempted among other investigations a study of the acquirement of precipitins against inoculated serum. The results, however, were not at all clear and such precipitins as were found were not specifically directed against the serum (i.e. were pseudo-precipitins).

We thus see that on the whole the work regarding the introduction of soluble protein into plants is not wholly satisfactory. The only positive results are those concerning anaphylaxis and these lose most of their significance because of the numerous failures of confirmation. Anaphylaxis or a process simulating it results from the sensitization of bacteria. In the higher plants, on the other hand, the evidence available indicates that anaphylaxis either does not occur or else it is governed by variables regarding which we as yet know very little. The precipitin technique should certainly be investigated in this connection. With the choice of suitable plants the technique is relatively simple, the precise nature of the antigen may be determined, and the results if properly controlled would be significant. The simplest

in theory and execution of the true antigen-antibody effects, it should have much to offer to the investigator in this field.

C. *Artificial introduction of corpuscular or particulate antigens*

Acquired immunity to the injection of corpuscles, bacteria, and similar corpuscular antigens may be exhibited in several ways, as through agglutination, lytic phenomena (lysis, antilysis, complement fixation), precipitation of extracts of the antigen, and if the antigen is living (*viz.* bacteria) alteration of its properties or lethal effects upon it. All of these manifestations of acquired immunity in plants have been studied by various investigators, and accordingly the present section will deal with them in turn.

First, as regards acquirement of agglutinins and lysins toward such antigens, the evidence is fairly abundant, although both positive and negative and both specific and aspecific results have been obtained. First in order of time are the results of Kritschewski (97) who in 1914 reported negative results from the injection of *Cotyledon* with bacteria. In 1921 Picado (141) found that injections of *Opuntia* cladodes with rabbit corpuscles or yeast cells induced neither agglutinins nor lysins. However, injection of this plant with corn pollen suspensions did result in the production of agglutinins and lysins. These pollenolysins were specific within the limits of the experiment, reacting strongly against corn pollen and pollen from other Gramineae (*Coix*, *Sorghum*) but not against that of plants more distantly related to corn; the agglutinins were less specific. Investigation of their properties showed that the pollenolysins were labile at 56°C. (15 min.), but there was also present a substance in fresh, non-immunized *Opuntia* juice (complement) which restored the reactivity to the heated extract. This work was repeated using lily pollen, but the results were not so satisfactory, since this is toxic to *Opuntia*. However, pollenolysins for lily pollen were at length obtained, active against the species of lily employed but not against other Liliaceae, yet also positive to *Gladiolus* (Iridaceae) and accordingly not family-specific as were the maize pollenolysins. In 1925, on the other hand, Carbone (38) repeated Picado's work with negative results. Carbone and França likewise failed in the demonstration of acquirement of agglutinins and lysins in leaf-extracts of *Drosophyllum*, a carnivorous plant which they had stimulated by feeding with sheep blood and with bacteria (48).

Carbone and Arnaudi did, however, succeed in the production of acquired bacterio- and haemo-agglutinins in *Morus* and *Prunus laurocerasus* in 1924 (45) using crude and elaborated plant *saps* (not *extracts*) as media to test for antibody content. These agglutinins were rather potent but non-specific, since for example a plant inoculated with cholera bacilli agglutinated this antigen less strongly than it did the Flexner dysentery bacilli. The agglutinins were coctolabile and relatively insensitive to pH. Accordingly these agglutinins are considered by these investigators as pseudoantibodies. At the same time a study of the acquirement of haemolysins and bacteriolysins failed to reveal the production of these antibodies in *Morus* and *Prunus*. The following year (46) these same workers reported further studies of antibody production in *Morus* and *Prunus*. When *Morus* was inoculated with suspensions of typhus and cholera bacteria and of *Bact. aterrimus*, the sap sometimes yielded acquired agglutinins but these were frequently non-specific. The results with the lytic tests were equally vague. When the crude sap was employed in place of the elaborated sap no acquired agglutinins

were demonstrated, but there did appear to be produced a sort of amboceptor which was highly thermolabile (destroyed by 1/2 hour at 56°C). In none of these cases was there any strong consistency in results nor specificity of antibodies. Accordingly these results confirm the earlier view of Carbone and Arnaudi regarding the pseudo nature of the antibodies. The same year Carbone (38) mentions having observed an antihaemolytic principle in potato which had been inoculated with sheep blood. On the other hand, Arnaudi in 1927 (6) observed in *Prunus* inoculated with typhoid bacteria the production of agglutinins which showed some degree of specificity, although the data given on this head are not very extensive.

Kořínek in 1922 (80) and Doussain in 1925 (56) were both unable to demonstrate the production of agglutinins or lysins in plants inoculated with bacteria. On the other hand, Much and Nyrén (127, 128, 129) have recently reported observations which seem to indicate that tubercle bacilli inoculated into living plants of certain species after several days become agglutinated *in vivo* and eventually dissolved. On the contrary the reaction does not take place in expressed sap. The various species of plants tested behaved differently in this connection, the bacteria in some instances killing the plants, in other cases surviving and propagating without injury to the host, and in yet other cases being killed without agglutination or lysis. The agglutinative and lytic principles here described, however, may have been normally present rather than acquired, and in addition their dependence upon the developmental condition of the plant (disappearing with death) has led Silberschmidt to suggest (161) that they may be merely of the type of the pseudoantibodies described by other workers.

Passing on to the subject of acquired antitoxins in plants we have the observation of Kořínek in 1922 (80) that saprophytic bacteria injected into certain vascular plants although not agglutinated nor dissolved become latent or inactive. That this may be due to an acquired toxin-antitoxin reaction is not improbable, but Kořínek's work offers no proof of this point.

Finally as regards the production in inoculated plants of substances which alter the morphological and physiological properties of bacteria or exert lethal action upon them, we are indebted to the works of Stickl in 1927 (168) and Much and Nyrén in 1930 and 1931 (127, 128, 129) for what little information is available. The former studied the effect of certain plants, notably *Tulipa*, upon typhus bacilli which were first inoculated into the plants and later reisolated. Using a great many cultures Stickl found that passage through the plant in many cases modified significantly the form and serological reactivity of the bacteria. This would appear to indicate that the plant has antagonized the bacteria by the production of substances modifying the structure and physiology of the latter. There is, to be sure, the alternate and equally sound hypothesis that such substances might have been normally in the plant and we thus are once again forced to accept the work only with reservations. The same comment applies to the work of Much and Nyrén, who found that typhoid bacteria injected into living plants of various species were in some cases so modified by the action of the host that their staining reactions, virulence, and serological reactivity became altered.

To summarize or separate the wheat from the tares in the present section is an exceedingly difficult task. We are confronted by several obstacles, failure in confirmation of experiments due to unknown variables, action of pseudoantibodies ren-

dering the acquired ones obscure, difficulty in determining whether certain positive reactions are normal or acquired, these and many other difficulties obscure the theme. A few facts, however, do stand out, for example that most of the reported cases of acquirement of antibodies deal with antibodies whose lack of specificity and other characters relegate them to the pseudo class, and that immunological phenomena *in vivo* may not be reproduceable according to the customary techniques *in vitro*. One very important concluson does follow from a consideration of these data, however, and that relates to the method of future investigation in this immediate direction. We cannot consider the problem as solved nor as much more than begun. We do know now of some of the difficulties in evaluating results. Accordingly the problem to be solved must be attacked according to some such procedure as the following:

a. The plants must be injected with antigens of determinate character, with controls, and in sufficient numbers to warrant statistical study.
b. Wide ranges of variation must be employed as regards techniques, quantity and type of antigen, species of host, time of extraction for antibodies, etc.
c. Observations must be made both *in vivo* and *in vitro* and these two carefully compared.
d. All obvious variables, genetic and environmental, must be rigidly controlled.
e. Normal reactions must be eliminated, preferably by the selection of species free from such reactions, or else by special techniques.
f. The specificity of the reaction must be ascertained by testing of the antibody extracts against a wide range of related and unrelated antigens.
g. The physical and chemical properties of the antibodies must be investigated with particular reference to protein reactions, molecular or colloidal size, thermolability or -stability, etc.

No one study before us has met all these various requirements, the omission of any one of which is fatal to a complete proof. It is neither theoretically nor practically difficult so to conduct an experiment that the results will be conclusive. One clear-cut experiment recognizing the variables pointed out above would be of more value than all of the evidence thus far secured, and it is therefore urgently to be desired that such experiments may be performed in the near future. It has been a revelation to the writer to analyze these experiments set forth in the preceding pages. Without such an analysis the field has appeared reasonably complete although somewhat contradictory in places. But on reviewing section after section of the subject matter it has been increasingly evident that there is hardly a single point which has been thoroughly investigated, and hardly one which would not be made transparent by a few carefully planned and executed experiments. A wealth of opportunity for research lies before us in this field. It is time to abandon the speculation and sketchy experimentation which have enshrouded the field and after a careful consideration of the outstanding sources of error to proceed systematically and thoroughly in the direction indicated by our perspective of the investigations thus far accomplished.

(*To be continued*)

PERIPATUS IN JAMAICA

By E. A. ANDREWS

"Peripatus is one of those animals whose presence lends a distinct character to the fauna of any region." WILLEY.

THE finding of Peripatus in a part of Jamaica B. W. I. not previously known as its habitat (incidental to a molluscan study aided by a grant from The National Research Council) may justify some consideration of the previously known distribution of this remarkable animal in that island.

The enigmatical nature of Peripatus was not fully appreciated till increased knowledge showed it presented in one animal traits previously known only in different groups; so that it was a puzzle such as might be some imagined simple animal showing the outside appearances of a dog along with, let us say, the internal gills of a fish. But finally it has become customary to place Peripatus in a distinct group of some fifty species approaching insects and centipedes, in a simple way, but with some features of annelid worms. They are found not only in the West Indies but in Central and South America, in Central and South Africa, in Australia and in Indo-Malaysia.

THE HISTORY OF PERIPATUS

Its worm-like appearance led to its being called an annelid and the two first known specimens in the British Museum were designated in manuscript *Nereis pedata* and *Nereis viridis* by two different zoologists, in the period when "Nereis" was rather a common name for many annelid worms. One of those two specimens was in the collection of Sir Hans Sloane, who was in Jamaica in 1687, but Bouvier concluded this specimen came from Dominica in the second half of the eighteenth century, toward 1760 probably, which, however, was seven years after the death of Sloane, at the age of 93.

Subsequently the first published account of the creature emphasized its resemblance to a mollusc, a slug; but this opinion was never taken up by any one else and for long the animal was assigned by some to the annelid and by others to the myriapod group, till wider knowledge of its anatomy and development furnished more complete evidence of its position near assumed ancestors of the insect group. That Peripatus looked like a slug was the impression gained by the Reverend Lansdown Guilding, when, long resident in the island of St. Vincent, he had in mind to write a complete fauna of the West Indies, but sought first to send back to England essays on all the main groups of animals looked at from three points of view: as injurious to man (*Pestes occidentales*) as objects of special wonder and interest (*Miracula zoologica*) and as being of direct use (*Usus animalium*). His contribution in 1825 belongs decidedly to the second category, for he there figures and describes the paradoxical creature he first named Peripatus. He found it by chance amidst plants he had collected at the foot of a certain great mountain. As one who had described certain new slugs apparently he saw in the slow movements, the possession of two retractile feelers, the soft velvety skin, along with the habit of ejecting glue-like material when disturbed, sufficient suggestions of slug life to overweigh the fact that the animal moved by distinct legs,

which, in fact, led him to the name Peripatus as having "ambulacra" or paired rows of legs like an avenue of trees and also induced him to place this animal into a new class "Polypoda;" thus, as he recognized, playing havoc with the group Mollusca that was well known to contain no animals with pairs of legs on the sides of the body. This sole specimen had 33 pairs of legs, all alike, and as it walked along on them like the common milliped, julus, he gave it the specific name *Peripatus juliformis*.

His excellent figures in color and concise Latin descriptions established the reality of this phenomenal animal without doubt, even though the author, in recognition of his remoteness from libraries, said: "I must request that, with the exception of the drawings, everything I may send back to England on subjects of natural history may be examined with the greatest caution and suspicion." Thus in Guilding's description under the heading Mollusca Caribbæana in the *Zoological Journal* of London, this problem creature was well introduced into scientific circles.

As years went by, other species of Peripatus were discovered in various West Indian islands, in South America and even at the Cape of Good Hope till finally in Jamaica, twenty years after Guilding's discovery, the well-known naturalist of the old school, Philip Henry Gosse, after his zoological work in England and in Canada, while then resident at Bluefields in the western part of the south coast of Jamaica, and well conversant with the animals of Jamaica, found five or six creatures that he recognized as like Guilding's Peripatus, but which, he thought, to be more like annelids than like molluscs. He found them when searching amongst stones in a burnt-over region not yet grown up with vegetation and close to virgin forest at the base of a conical peak in the mountains four or five miles from Bluefields.

Three of these lasted on in the British Museum to be studied in succession by three authorities. Nothing more was known of Peripatus in Jamaica for nearly fifty years, but then in 1892 a local naturalist versed in the study of insects, Mrs. E. M. Swainson, found some seven Peripatus on Beacon Hill about a mile from Bath, in the eastern part of the island and thus more than a hundred miles from Gosse's Bluefields. Some of these specimens were sent to the headquarters of science and art in Jamaica, The Institute of Jamaica, where they were studied by Dr. M. Grabham and by T. D. A. Cockerell, who noted such differences from the account of Guilding that they decided to recognize a new species *Peripatus Jamaicensis*.

The region of Bath has since then remained the chief source of knowledge of this animal in Jamaica; but in 1897 when the Johns Hopkins Marine Laboratory was located at Port Antonio, on the north coast, when a chance outbreak of yellow fever caused the death of both Professor Humphrey and the zoologist of promise, Dr. Conant, the latter found one specimen of Peripatus at Blue Hole, to the east of Port Antonio, thus adding a third locality situated 120 miles from Gosse's and 15 from Bath. Thus Peripatus was known at points in a large area, but yet very few specimens had ever been seen when in 1901 a request for more specimens to be sent by Ray Lankester to Professor Bouvier for use in his great monograph of the Peripatus species of the world, was met by activity at The Institute of Jamaica. J. E. Duerden found that after the original seven sent in 1892 from Bath to the Institute a dozen more reached Dr. Grabham in 1893 and after that but two or three were found in scattered localities; they seemed rare indeed since collectors could find

none. Advertisements in the papers brought no results; but when Dr. Duerden collected some and exhibited them with offers of reward, the natives soon found them in large numbers; 50 were brought in and Dr. Grabham also obtained a large supply; then eighty more came, and fifty more were offered. All these were found under stones and rotten wood and often buried in the earth. By comparative study Professor Bouvier found that some 24 of these specimens were properly to be called *Peripatus jamaicensis*, but some 72 were a variety of Guilding's *Peripatus juliformis*, to be called var. *Swainsonae*. Gosse's original specimens also proved to be of the same two; and all the specimens thus far found in Jamaica are referred to these same.

A NEW LOCALITY FOR PERIPATUS

In March and April 1909, Thomas Barbour demonstrated the abundance of Peripatus near Bath by finding some hundred specimens. A fourth locality for Peripatus in Jamaica was found in 1910 by the present writer, at the head of row-boat navigation in the Great River to the east of Montego Bay on the north coast, less than 20 miles from Gosse's place of discovery and 100 miles from Bath; thus establishing the existence of Peripatus at the four corners of a great quadrilateral one hundred miles long and fifteen to twenty wide; however, only a single specimen was obtained at each of the north coast localities. Within this major area of some 2000 square miles, nearly half of the area of the island, no localities for Peripatus were recorded till the present July 29th, when one specimen was taken in searching for small molluscs amidst dead leaves in a region along the road from Kingston to Stony Hill, so often traversed as on the way to Castleton Botanic Gardens. This new locality is twenty-five to thirty miles from the two known localities in the east and about eighty from the two in the west part of the island that form the corners of the above mentioned quadrilateral. This fifth locality is but little above Constant Springs and not five miles from Half Way Tree, in fact scarce seven miles from the Institute of Jamaica, but though so near the center of a dense population it is perhaps secure from destruction, as being along the water-works reservation.

More precisely described, this new locality may be found by leaving the road below the bend by a gate on the right at a sign marked by the Board of Public Works. A trail here leads up along the water pipe and then along the open "gutter" carrying water from the Hermitage dam presumably. About 440 paces from the gate the trail bends to the right as we note a low arch in a wall allowing water to pass across the road down to the right, on occasion: here, on the left, lie large exposures of rough limestone, on top of which the Peripatus was found amidst dead leaves shaded by the dense brush of the hillside. Removing leaves the Peripatus was accidentally seen partly projecting from under the dead leaf and taken to be perhaps a slug, but as when picked up it discharged its glue in fine threads adhering strongly to the fingers, clear and nearly tasteless, and moved with caterpillar-like legs, while in the light revealing the beauty of its velvety skin, it was recognized as Peripatus. Allowed to crawl on the hand it quickly sought the under, shaded side and in a bottle amidst dead leaves it came to rest out of the light. Search for another specimen was fruitless, but the time available was but scant.

PERIPATUS AS A TRAVELLER

Amidst these dead leaves in the bottle with much moisture and frequent airing

it lived on not only the few hours before sailing but all the trip to Baltimore and then in a larger glass dish it kept its quiet existence till September 8th.

Though this is the first living Peripatus to emigrate from the West Indies, Dr. Grabham saw living Peripatus from New Zealand and the Cape at Cambridge with Professor Sedgwick, who states that he went to the Cape in the middle of August, 1883, collected and brought back over three hundred living Peripatus, of which some lived on till the following July; while Walter Heape brought back some more living ones in 1884 and another large shipment of living Peripatus collected at Table Mountain was sent on in the winter of 1884–5. Moreover, while two successive attempts to import living Peripatus from New Zealand to Cambridge were not successful, since the animal died on the long voyage, yet a third attempt succeeded when the Peripatus were kept in a special cool part of the ship. Two of these went a further journey to Würzburg. Living Peripatus were kept in the museum in South Africa where Sedgwick saw with astonishment the 30 or more young just born and some of them crawling upon the back of the mother.

Bouvier also received one living Peripatus sent from the Cape to Paris in a small box full of wet moss. This specimen was then kept in a glass dish with the moss, earth and bits of decayed wood till it finally escaped from under the lid, after being studied for some time. Other specimens have been carried home and kept alive. In Australia, Fletcher kept one Peripatus alive for three or four months, in a tin; he also collected and brought home 100 healthy specimens, many of which were kept nearly a month, during which time they gave birth to young; but in some very hot weather they developed blister-like swellings on the head, and then were killed. Evans in the Malay Peninsula chopped into dead stumps and found Peripatus dormant within dry wood 4–5 feet above ground and also found them in fallen logs. But in South America he reports a native found Peripatus amidst dead and decayed tree trunks and leaves and nine specimens brought to Georgetown, British Guiana, were kept alive in a glass jar kept very wet, as in an artificial swamp. Another American species was also kept alive in these very wet conditions. Previously in that region Slater had found Peripatus exceedingly scarce under rotten logs and decayed palm stalks, but had taken 20 of them from Demarara to England alive, but suffering from cold.

In Trinidad, Kennel observed that though usually but one Peripatus was to be found isolated here and there yet in a very dry season 60 were found under one small decayed branch where they had sheltered to avoid the dryness of day. He also kept dozens of Peripatus in tins with rotten wood for weeks without food, but when too dry many died, yet others revived in wet air, though they avoided liquid water. Later some of these revived specimens took the long journey to Europe though here again some died after four weeks when sufficient moisture was accidentally omitted; others arrived alive and one of them went on to Würzburg to be kept alive in Semper's greenhouse.

In Jamaica, however, Peripatus has not been a good traveller, for while Grabham and Cockerell say of the three specimens sent by Mrs. Swainson to Kingston that one was still alive, this was a great exception; in fact Barbour makes use of the delicacy of Peripatus to strengthen his arguments that Jamaica had not been stocked by chance transport of animals over the sea but by migrations over land connections formerly existing. He says:

Peripatus is one of the most delicate of known organisms. Dr. Grabham, a well known field naturalist, long resident in Kingston, Jamaica, tells me that with the greatest care he had never been able to bring living Peripatus from Bath to Kingston, a distance of 35-40 miles and my experience has been exactly the same. Last winter it was found absolutely impossible to keep alive at all any of the hundred-odd specimens which were taken in the vicinity of Bath. On the return from a day's collecting many dead specimens were always found in the receptacle in which they were carried, which was filled with the natural earth and moss taken from the spot where the creatures were found.

Conceivably these Jamaica Peripatus might have travelled better had they the extreme moisture and avoidance of heat that is reported as necessary for some other kinds of Peripatus on long journeys; moreover, the presence of coiled dead leaves within which the Peripatus may lie concealed may be of aid in transportation as well as in normal life on the forest floor.

While the present solitary specimen shows that long journeys may be made on shipboard without death, whether a Peripatus concealed within a tree trunk could be carried, floating, across salt water can scarcely be decided till experiments have been made to test the resistance of Peripatus to salt water. Excepting for contact with salt water the air, water, moisture, temperature, conditions within a tree trunk and within a bottle on shipboard seem not so very different; and enveloped in a film of air could the animal escape contact with salt water? Gosse said of the specimen he found "The skin repelled both water and spirit when immersed." Likewise Willey found that Peripatus collected in the island of New Britain floated on water and when immersed was covered with a beautiful sheen of air. Similarly this last specimen from Jamaica, though living amidst very wet leaves, always remained dry, supported on its legs above the water and protected by the peculiar skin surface and when dead it floated on Carl's solution and when shoved under was coated dorsally by a thin film of air, as in some diving insects, stretched over its rows of papillae, and collected in larger areas just above the bases of the legs; but the shrivelled antennae held no air.

As a witness against the old "flotsam and jetsam" theory of the peopling of such islands as Jamaica, Peripatus stands in need of further cross questioning. Could it be shown that migrant birds transport living snails, one might invoke Peripatus glue and coiled dead leaf as aids to such aerial transport. Once transported a single pregnant female might populate a new region.

DESCRIPTION AND BEHAVIOR

The present successful Jamaican specimen is of full size for the species, stretching out alive to 75 mm. and dead 74 mm. with width and depth of about 5 mm. while the antennae were elongated by the animal to 7 mm. but in death shrivelled to scarce 3 mm. Alive, the plump well-fed appearance of the animal is enhanced by the rich velvet of skin which excels in the Jamaica Peripatus, for Sedgwick, after expressing great admiration for the beauty of Peripatus, said of the Cape species: "These animals so far as skin is concerned are not surpassed in the animal kingdom." And yet Dr. Grabham who saw those same Cape specimens remarked of the Jamaica species; "In point of beauty the skin certainly surpasses both the New Zealand and the Cape species."

The color of the present specimen was greenish mixed with brown; the transverse rows of tubercles on the back being yellow with dark-red-black central spines and with pale green transverse grooves in advance of the tubercles; the underside was pale flesh color. The antennae did not have the white tips common in *P.*

jamaicensis and the skin sculpturing together with the 34 pairs of legs led one to identify it as a female specimen of *P. juliformis* var. *swainsonae*. When placed after death into Carl's solution, which contains acetic acid, the green color rapidly disappeared, leaving a dull maroon, much lighter below and this persists in alcohol.

Like all known Peripatus, this one in Baltimore showed the strongest negative reaction to light, walking rapidly away whenever light fell on its head, or going backward to escape it; being active only at night and remaining all day concealed under dead leaves or buried in rubbish. Its marked habit was to select some coiled-up leaf and to rest within its protection lying on the dead leaf and covered by its coiled-over part. Thus concealed it was difficult to find in a dish of leaves, especially as it remained quiet when the leaves were moved about. No doubt such hiding within coiled dead leaves would make discovery of specimens on the forest floor very difficult.

At rest, this Peripatus was not seen to coil up with ventral side inward, as seen by Bouvier in a certain species, but was coiled back and forth in various shapes with ventral side down, as a rule, though the body might be twisted so that some of the legs were uppermost. Moving about outside its resting place it showed a tendency to walk along the edges of solid objects and the same preference for contacts seemed shown in the habit of moving along on its own body; that is, it adopted many attitudes of hooks and parallel lines as it turned its head backward and crawled along itself. It was not seen closely coiled but a cross section might have shown its body cut three times. Within its preferred leaf lodge it would readily turn end to end like a myriapod or many other animals used to dwelling within cavities.

Placed out in the light it walked with raised head swaying from side to side, testing everything with its antennae, as described by Bouvier. Each leg swung back a wide arc, broke suddenly from its attachment and passed swiftly forward close to the preceding foot, which is raised as the advancing foot is clapped down in its most forward position to anchor to the substrate.

Quite like some insects, the Peripatus was seen to clean its antennae with its mouth, but it elongated them and bent them down like an elephant's trunk to draw them through the mouth which was everted to show the jaws. First one, then the other antenna was thus treated.

THE FOOD OF PERIPATUS

Knowledge of the natural food of Peripatus remains unfortunately very meager. The chief record of direct observation is that of Capt. Hutton in 1876 who found Peripatus in New Zealand in decayed wood, under stones or in crevices of rocks and kept them under observation, stating that they do not feed in winter though still breeding and that they feed in the night but also in the day time when hungry. He says "I have seen one shoot out its viscid fluid from the oral papillae at a fly introduced into the jar in which it was confined and stick it down; it then went up and sucked its juices, rejecting the whole of the integument."

Sedgwick in 1888 said that of the food in nature we know nothing but that in Cambridge Peripatus ate the entrails of their fellows and also their embryos and also liked raw sheep liver. Bouvier found in dissecting many specimens of several species chitinous fragments of insects, but also pieces of vegetable tissue he thought might have been in the food of the creatures eaten by Peripatus. He failed to induce the captive Peripatus to eat earth-

worms or wood-lice. Kennel was not certain, but thought that Peripatus ate little termites and also snails and little worms; but he never saw them eat. In captivity his Peripatus ate drops of its own glue and Kennel inferred that in nature it may eat its prey and glue at the same time.

Nothing is directly known of the food of the Peripatus in Jamaica. Cockerell speaks of their casting out glue in a network that holds the insects used as food, but, as Bouvier remarks, it is not clear that this was direct observation upon Jamaica specimens, but it seems rather part of Cockerell's account of the habits of Peripatus in general.

In Baltimore attempts to feed with pieces of earthworm and crushed insects were apparently without success; on the other hand there was as considerable evidence that the animal bit out pieces of dead leaf; and fragments of dead leaf, as well as very small amounts of insect remains, were found in the faeces. Possibly the reported long continuance of Peripatus in good health without apparent food, but with presence of decayed wood and the like, may be in part due to some ability to use dead vegetable matter as food.

A few days before its death this Peripatus was transferred to a large formicary, 7 mm. deep, in which it walked some 42 cm. through a zig-zag passage from the light to take up its abode in a coiled leaf, see Figure 1. From this place farthest from the window-light, screened by opaque paper it apparently walked back at night to the point of ingress and ate from a slice of apple a depression 4 by 4 by 2 mm. A small bit of the apple, 2 by 1 mm. was found close to the head end of the animal, outside the leaf, the next day, when the Peripatus was back in its leaf, but dead. Examined that night by red light without other disturbance the Peripatus discharged its glue from the head end and then from the hind end of its retreat as if irritated by the light, but the next day three small red ants were found dead, within the leaf close to the Peripatus as if they might have been involved in the irritation.

The discharge of glue when irritated is one of the remarkable responses of Peripatus. Evans in the Malay Peninsula saw a captured Peripatus cast its glue 18 inches. Kennel says in other species the glue is thrown two to three feet and

FIG. 1. DEAD PERIPATUS WITHIN CURLED OAK LEAF ON RIGHT, HEAD CONCEALED, TAIL ABOVE, REMOVED ON LEFT OF MILLIMETER SCALE

striking an obstacle spatters to form a network of fibers, but, though sticking on one's hands so that it cannot be removed without soap and water, it does not adhere to Peripatus itself. This present specimen discharged its glue several times when picked up at long intervals; once making on the finger under a bit of dead leaf a puddle 5 by 5 by 2 mm. that held the 14 grams weight of metal forceps. The long glue threads stretched between one's fingers spring back like rubber and are beaded with small drops each of which when touched

with a needle can be drawn out as a long side thread. Apparently this should be very effective for entangling small insects.

THE DISTRIBUTION OF PERIPATUS

Returning to the known distribution of Peripatus in Jamaica we gather from the maps of R. T. Hill that the five localities where it has been found are about the 1000 foot level, or below it; while in Australia, Peripatus has been found all the way up to 5700 feet where it was collected by Fletcher in regions where for 4–5 months snow lies several feet deep. Moreover, in two of the above five localities in Jamaica it was closely associated with rough limestones and probably so likewise in the original locality near Bluefields, as well as in the locality at Blue Hole, but in the fifth where most have been found the rocks are much more complex; though there may be some hard limestones there. This Bath region is on the older Eocene and Cretaceous formations but all the other localities on the prevailing Oligocene limestones of deep sea origin, though the Blue Hole occurrence may have been on recent raised coral rock.

Possibly Peripatus may live in some of the regions of Jamaica where not yet known, but that Peripatus may occur in all or much of the region intermediate between the five known points is by no means certain. In two localities apparently alike, Willey found Peripatus in only one and remarks: "the extremely local, or sporadic, occurrence of Peripatus is well known."

SUMMARY

The finding of Peripatus in a fifth locality in Jamaica shows that it ranges sporadically over near half the island at elevations under, or near, 1000 feet, often on limestone formations, in damp woods, on or in dead wood and earth and dead leaves especially.

Previous inferences that the Jamaica Peripatus species were excessively delicate and impossible to transport alive need to be modified, since this last discovered specimen was brought to Baltimore and kept a month in captivity. In the past other species in New Zealand, South Africa, Trinidad, South America and Australia have been carried long distances and kept in captivity.

Inferences that Peripatus could not possibly be disseminated from land to land across seas are not entirely binding, but await experiments as to the ability of Peripatus to remain alive if exposed to salt water.

While the food of Peripatus remains still too largely unknown, this Jamaica specimen offered some hints that dead vegetation may form a part.

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THE FLORA OF THE HAWAIIAN ISLANDS

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THE study of the vegetation of any region, its composition and relation to its environment may be of great interest to the botanist; but far more important is a study of the origin of the plants composing the flora and their relationships with those of other parts of the world. Such studies may furnish important data, both to biologists and geologists, as they often throw light upon changes in land connections and the corresponding distribution of the waters of the oceans, such changes involving marked climatic effects as well.

In some extensive areas in the north temperate zone, the history of the vegetation is revealed both by a study of the living plants, and the fossils. It is evident that the northern parts of both Eurasia and North America have been more or less intimately connected from a very remote period.

Throughout this whole region, from Western Europe to Canada and New England, the predominant trees are much the same—pines and firs, poplars, willows, birches, maples, oaks, etc.—and the shrubs and herbs show a similar relationship. While there are many differences in detail, the essential character of the floras is the same. Where there are marked differences a study of the fossil plants shows that some of these are due to the extinction of once widespread types which are now greatly restricted in their range. The Californian Sequoias, the bald cypress of the Gulf States, and the tulip tree (Liriodendron), are examples of such once cosmopolitan trees.

The conditions in the south temperate zone are very different, and the widely separated continental areas—Africa, South America and Australia,—differ much more from each other than is the case in the north temperate zone. Moreover our knowledge of the fossil plants of these regions is still very incomplete.

The floras of these isolated regions show a high percentage of endemic species, and this is also the case in such large islands as Madagascar, Juan Fernandez and New Zealand. It reaches its most extreme expression in the Hawaiian Islands, the most isolated area of equal size in the whole world.

The Hawaiian Archipelago consists of a chain of islands extending from northwest to southeast, between latitude 18°55′ and 21°15′. Its total area is 6,454 square miles, of which the southernmost island, Hawaii, comprises about two-thirds. To the northwest, there is a series of small islets and reefs, extending for about 18 degrees. All of the islands, except for the coral reefs, are volcanic; but at present volcanic activity is restricted to Hawaii, whose two giant craters, Kilauea, and Mauna Loa, from time to time furnish volcanic outbursts of spectacular proportions.

. In the older islands no evidences of recent activity can be found, and the disintegration of the volcanic soils is complete; in Hawaii, however, and to a lesser degree elsewhere, there are expanses of bare lava, nearly or quite destitute of vegetation.

The volcanic activity has evidently

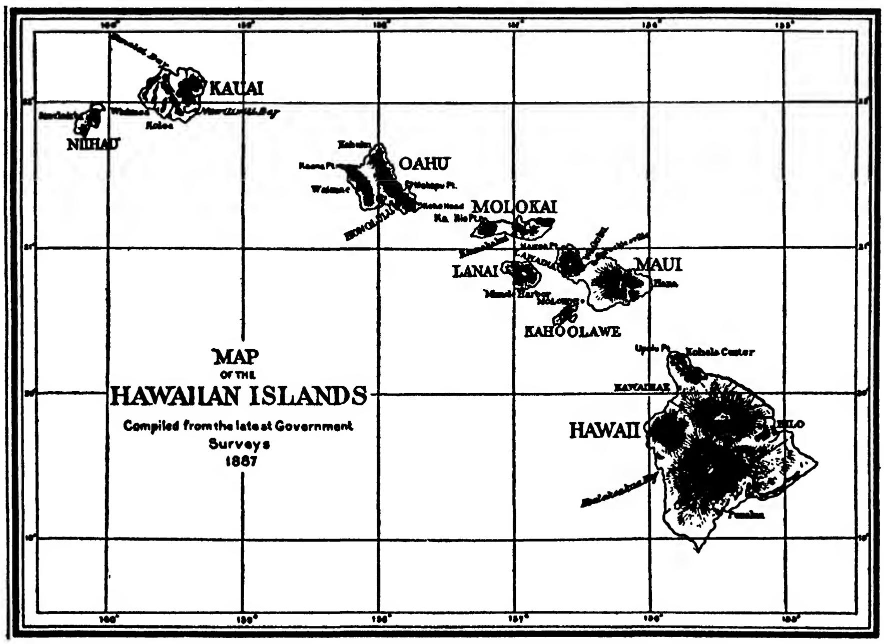
developed along a rift beginning at the northern end of the archipelago, and has proceeded southward, and now is found only in the active craters of Hawaii.

There is abundant evidence that the larger islands were formerly united into a single much larger land-mass, which through long subsidence has gradually segregated the existing islands. That the northern island, Kauai, was first detached, is indicated both by the deep and broad channel between it and its neighbor to the south, Oahu, and also by its very highly specialized flora, the proportion of endemic species being greater than in any other island.

Upon Oahu is Honolulu, the main city of the territory. Between Oahu and Hawaii are Molokai and Maui. Two smaller islands, Niihau, off the coast of Kauai, and Lanai, near Molokai, may also be noted.

The topography, especially in the older islands, is excessively rugged. The windward districts are drenched with torrential rains, deposited by the moisture-laden Northeast trades. The resulting erosion has cut deep and precipitous canyons with almost vertical walls, "palis" in the vernacular, whose brinks, concealed by dense vegetation, are a serious menace to the incautious explorer.

The effects of erosion on the windward coast of Hawaii are very evident as the steamer approaches. The openings of deep gorges are visible, cutting through the high vertical cliffs, and often discharging a cataract which plunges into the sea. The writer visited the head of one of the largest of these canyons, Waipio Gorge, whose vertical walls are 3,000 feet deep. Over the edge of this canyon, cataracts fell, reminding one of some of those in Yosemite.



In the older islands, e.g. Kauai, Oahu, the mountains are much worn down and the highest summits are only 4,000–5,000 feet elevation. In the most recent islands,

Maui and Hawaii, the great volcanic cones are much higher, Haleakala on Maui being 10,000 feet, and Mauna Loa and Mauna Kea nearly 14,000 feet. The latter (13,675 feet) is the loftiest peak in Polynesia.

On these high islands nearly all the moisture is precipitated on the windward (N. E.) side, but in the lower islands much of the moisture is carried over the mountain summits and falls on the lee side. This is well shown back of Honolulu, where the heaviest rainfall is at the head of the valleys on the lee side of the mountain range. The shore, however, is much dryer, and may be even arid, so that the contrast between the scant vegetation of the lee shore, and the rank vegetation of the rain-forest at the head of the valleys, is sufficiently striking.

Owing to their extreme isolation, separated by 2,000 miles of ocean from the nearest land mass of any size, there is an exceedingly high percentage of endemic species, many of them extremely specialized and testifying to a long period during which evolution has been active with little disturbance from outside.

Except for the almost exclusively volcanic nature of the soils, which has doubtless been a factor in the evolution of the flora, the conditions are extremely varied. With elevations ranging from sea level to nearly 14,000 feet, there is a corresponding range of temperature from tropical heat in the lowlands, to regions almost of perpetual snow. The variation in rainfall is equally striking, ranging from an annual rainfall of 400–500 inches to less than 20 in some of the dry leeward districts. These extraordinary ranges in elevation, temperature and precipitation, occurring within so limited an area, afford the biologist an unusual opportunity for studying a wealth of problems of the greatest importance in plant evolution. Considering the latitude the temperatures are very moderate.

Unfortunately for the botanist, much of the original vegetation in the lower districts has disappeared since the advent of the white man. During the past fifty years nearly all of the available land at the lower elevations has been brought under cultivation, and the forests have disappeared. The ravages of cattle and sheep, and in the dryer parts of the islands, goats, have also completely denuded large areas, formerly covered by forest. Through these agencies doubtless certain species have been quite exterminated. Moreover the introduction of many foreign plants, such as lantana, guava and many weeds, which are completely naturalized, has entirely changed the aspect of the vegetation in many places.

Practically all of the arable land in the lower areas is under cultivation and the huge plantations of cane and pineapples monopolize most of the land not occupied by rice fields, taro patches, and home gardens. Most of the conspicuous trees, shrubs and weeds are introduced, and give the casual observer an entirely erroneous impression of the indigenous flora. About Honolulu, for example, two very common trees, the "Algaroba" (*Prosopis juliflora*), which was first planted more than a hundred years ago, and the "ironwood" (*Casuarina equisetifolia*) a later introduction, seem to be thoroughly naturalized, and might very well be supposed to be really natives. Many foreign weeds are thoroughly established, and in the hills back of the city, one encounters almost impenetrable thickets of lantana and guavas—escapes from gardens which have become veritable pests. In the dryest places prickly pear cactus, introduced from Mexico, and a thorny Acacia (*A. Farnesiana*) are abundant. In the moister places, some very attractive exotics have

become naturalized. Wild ginger (*Hedychium coronarium*), cannas, morning glories, passion flowers, are common along the roadsides and in the woods and the moist valleys back of Honolulu.

The climate permits the cultivation of most of the tropical fruits—mangoes, avocados, papaya, custard apples—and many others, and a profusion of showy flowering trees and shrubs adorns the gardens. Among the shrubs, especially in Honolulu, are many varieties of Hibiscus, some of which are hybrids of the common *H. rosa-sinensis* with some of the native species.

As might be expected from the extreme isolation of the Archipelago, both the flora and fauna are highly specialized and the percentage of endemic species is very large. According to Hillebrand (25) 75.93 per cent of the indigenous vascular plants are endemic, while no less than 85 per cent of the dicotyledons are confined to the islands. This high degree of endemism is confirmed by later studies. According to a recent enumeration of the flowering plants, furnished me through the kindness of Mr. E. H. Bryan, Jr., of Honolulu, a total of 1,052 indigenous species of flowering plants is given. Of these 163 are monocotyledons, 889, dicotyledons. Of the former 119 species are endemic, of the dicotyledons 832. This extraordinary degree of endemism is probably unequalled in any other region of the world. A somewhat similar condition obtains in New Zealand, but perhaps owing to the much cooler climate, the number of species, especially of dicotyledons, is relatively less than in Hawaii. The latter, although only about 1/16 the area of New Zealand, has approximately two-thirds as many species. According to Cockayne (16), the total number of vascular plants in New Zealand is approximately 1,780, and the percentage of endemism nearly as great as in Hawaii, viz., 74 per cent for all the vascular plants, and 85 per cent for the dicotyledons.

There are two very different theories as to the origin of the archipelago. Hillebrand (25) and others believed that the islands were elevated above the sea through volcanic action starting in the ocean depths, and that they have always been completely isolated. At present the water of the surrounding ocean is very deep. Within forty miles, depths of upwards of 10,000 feet are found, and between the islands and the American coast is an enormous area of very deep water, in places exceeding 20,000 feet.

There are other students, however, who, in spite of the deep water now surrounding the islands, believe that they have not always been so completely separated from other bodies of land. The advocates of this theory assume that the islands were united into a much larger area than at present, and that this was connected, more or less directly, with the Australasian and Malayan regions in the Southern Pacific. The multitude of islands constituting Polynesia is believed to be merely the remnants of once much more extensive land-masses, possibly of continental dimensions, so that these scattered islands are the remains of mountain masses that have been in subsidence possibly since early Tertiary times.

While between Hawaii and North America there is an enormous and continuous area of very deep water extending north and south of the chain of islands, on the west there is a shallower opening continuous with a large area of lesser depths comprising the greater part of Polynesia. To the southwest are two large shallow areas including respectively the Marshall and Caroline Islands, presumably the remains of much larger sunken land-masses. A chain of similar but

smaller shallows extends to the Malay Archipelago, and it is possible, at least, that this indicates the line of connections between Hawaii and the lands in the Southern Pacific.

As to the period at which Hawaii became completely isolated, it could hardly have been earlier than the Upper Cretaceous or early Tertiary, since, so far as we know, few of the modern angiosperms existed prior to the Upper Cretaceous.

The discovery of the Hawaiian Islands is usually credited to Cook, although it is not unlikely that some of the early Spanish voyagers may have touched at the islands. Cook first landed in 1778, and again a year later, when he was killed by the natives. In 1792–94, Vancouver visited Hawaii, and collections of plants were made, and in 1816, Kotzebue also visited the islands and collections were made by Chamisso (13), who also collected along the American coast and who discovered and named the Californian poppy, Eschscholtzia.

From the first settlement by Americans, in 1820, the study of the native flora has been encouraged and many important contributions have been made. In 1888 was published a comprehensive flora by Dr. William Hillebrand (25), who spent some twenty years in the Islands. This flora described 705 species of indigenous flowering plants, and 155 pteridophytes. Many additions have been made since the publication of Hillebrand's flora.

My first visit to Hawaii was in 1892. I was especially occupied in collecting material of the tropical pteridophytes and liverworts for a work on the archegoniates upon which I was then engaged, and comparatively little attention was paid to the higher plants. Some years later, during which time I had collected in the East Indies, the Islands were again visited, and I noted the occurrence of a number of liverworts apparently identical with Malayan species. Especially striking was the abundance of a conspicuous species, *Wiesnerella denudata*, indistinguishable from specimens collected by me in Java, and known elsewhere, except for Hawaii, only in northern India and Japan.

About this time, my attention was directed to the studies of Dr. H. A. Pilsbry of Philadelphia, on the land snails which are such a notable element in the Hawaiian fauna (34). Pilsbry states that these are very old types, now mainly restricted to Polynesia, but related to species of the adjacent Asiatic regions. Pilsbry believes that these primitive snails are relicts of an ancient fauna which have survived from a period when Hawaii was part of a continental area connected with the Polynesian area to the southwest. He thinks it impossible that these snails could have reached the islands from without, whether by birds or drift, or any other agency, since some of these agents would also have introduced some of the modern snails or slugs, none of which are known to be indigenous.

This at once suggested to me that the liverworts might offer a similar problem, and it seemed worth while to see how far the flora as a whole confirmed Pilsbry's conclusions. The result of this investigation was rather surprising. It was evident that a very large majority of the flowering plants were clearly related to the floras of the Southern Pacific, including New Zealand, Australia and the Malayan countries, while the American relationships were relatively few. These facts strongly supported Pilsbry's conclusions as to some more or less direct connections which once existed between the Hawaiian Islands and some much more extensive land areas to the southwest.

BOTANICAL REGIONS

The plant-formations in the islands are of several well marked types. Rock (35), who has given a very satisfactory account of these, recognizes six principal formations: 1. Strand flora; 2. Lowland; 3. Lower forest; 4. Middle forest; 5. Bog region; 6. Upper forest.

Strand Flora

Sandy beaches are not extensively developed, as the shore, especially in the more recent islands, is often composed of extensive recent lava flows, or steep broken cliffs, both unfavorable for the growth of maritime plants. This is true also for the beaches covered with broken lava boulders and pebbles. In the older islands, like Oahu and Kauai, there are beaches of coral sand, like the famous beach of Waikiki.

The strand flora is much less developed than in most tropical islands like those of the South Seas and West Indies. As in the East Indies, a conspicuous small tree is a screw-pine (*Pandanus odoratissimus*). Another small tree, found on most tropical beaches, is the "Hau" (*Hibiscus tiliaceus*). Other characteristic trees are *Calophyllum Inophyllum* and *Terminalia catappa*, also cosmopolitan strand species. Other cosmopolitan strand plants are *Ipomoea pes-caprae*, and *Scaevola frutescens*. A number of other wide spread species might be added—e.g., *Heliotropium curassavicum*, *Ruppia maritima*, *Scirpus maritimus*, etc. With these are some endemic species which are, however, usually somewhat local in their distribution. Such are two species of Schiedea, (Caryophyllaceae) and Brighamia (Lobeliaceae).

None of the trees and shrubs of the strand region are confined to it, and the line between the strand and the lowland above it is not at all clearly marked, many strand plants invading the lowland area, and *vice versa*.

Lowland Zone

On the lee side of the islands the lowland area is mostly open grassland, but even where it is not under cultivation, it has been invaded by introduced trees, especially in the neighborhood of Honolulu. The Algaroba, already referred to, and *Acacia farnesiana*, are perhaps the commonest. Fringing the beach near Waikiki, the groves of Casuarina recall the beaches of the East Indies, where it is one of the commonest strand trees.

According to Rock the most abundant of the native lowland grasses are *Andropogon contortus* and *Panicum torridum;* but many alien weeds have largely ousted the indigenous plants. In the dryer places the prickly pear (*Opuntia tuna*) has taken possession, and also lantana, both escapes from cultivation. The latter, however, is by no means confined to the lowlands, but has spread over the forested areas, up to 3,000 feet or more. The Mexican poppy, *Argemone* (sp. ?) is a showy plant of the lowlands.

Lower Forest

This extends up to 2,000 feet elevation. There is naturally a marked difference in the character of the forest on the windward and lee sides of the islands. On the windward side of Hawaii, for example, the steep cliffs are forested to the water's edge, and there is a typical rain-forest of great luxuriance, but less rich in species than the dryer lee forest.

Two trees, possibly not truly indigenous, are the most numerous in the lower forest. Approaching Honolulu from the sea, the eye is at once arrested by patches of pale green in the dark green forest mass

covering the base of the mountains. This light green foliage belongs to the "Kukui"—*Aleurites moluccana*, which with the "Ohia" *Jambosa malaccensis*, make up a considerable part of the lower forest. Associated with these are many endemic shrubs and trees. One of the most important of these is "Koa," *Acacia koa;* others are species of Straussia, Gardenia, Bobea, Sandal wood (Santalum) Pisonia, and others. Also, but more abundant at higher elevations, is the "Ohia lehua," *Metrosideros polymorpha*, perhaps the most wide spread of the Hawaiian trees.

The lower forest on the leeward side is quite different in character. The soil is usually more or less arid, and there is a scanty undergrowth, and a marked scarcity of lianas and epiphytes. Of the former are species of Caesalpinia, Cocculus and Sicyos. Two parasites are common, a mistletoe, *Viscum articulatum*, and *Cassytha filiformis*.

There are many more species in this dry forest, and among these are some of the most characteristic Hawaiian genera. The Araliaceae, e.g., Reynoldsia, Tetraplasandra, Cheirodendron, notable features of the Hawaiian flora, are especially developed in this lowland forest. A very common tree is the liliaceous *Dracaena aurea*, which resembles a tree Yucca, or the New Zealand *Cordyline australis*, often planted in California.

A few of the trees shed their leaves during the dry season but most of them are evergreen. One of the commonest deciduous trees is *Erythrina monosperma*.

The species of the mixed lowland forest are for the most part the same in all the islands, but there are a good many local species, often of very limited range.

The Middle Forest

The lower forest merges gradually into the middle forest zone, which extends to about 5,000 feet elevation. This zone is for the most part a pronounced rain-forest and in the windward areas receives an enormous rainfall. In this wet forest the vegetation reaches its maximum luxuriance.

In the mountains back of Honolulu are several valleys in which there still may be found a considerable amount of forest. As the mountain range is only about 3,000 feet high, the rain winds pass over the summit and heavy rains are deposited in the valleys. It may be as much as 200 inches annually while a few miles away, in the coastal area, it is less than one-fourth as much.

McCaughey (27) has given a good account of the vegetation of Mauoa, the largest of these valleys. Most of the lower forest has disappeared, but the head of the valley still harbors much of the original forest.

Where the lower forest still exists it is composed mainly of Kukui (Aleurites) and Ohia (Jambosa). Above the Kukui zone is a region characterized by another important native tree, *Acacia koa*, allied to the phyllodineous Australian species. Above the Koa zone is the rain-forest in which are found many characteristic, mainly endemic, trees and shrubs. Among these are species of Antidesma, Cheirodendron, Eugenia, Ilex, Hesperomannia, Metrosideros, Osmanthus, Pelea, Pittosporum, Santalum, Pritchardia, Suttonia, Cyanea, Coprosma, Hibiscus and others. This wet forest abounds in liverworts, mosses and ferns.

While some species like *Acacia koa* and *Metrosideros polymorpha*, occur in all the islands, each of the larger islands has many species peculiar to it. The percentage of these endemic species increases with the age of the islands, and attains its maximum in Kauai. The latter is therefore, of especial interest to the botanist.

The greater part of this island is occupied by a plateau of about 4,000 feet elevation, rising in the center to 5,000 feet in Mt. Waialeale. This mountain receives the extraordinary rainfall of about 500 inches annually.

The ascent from the lowland to the plateau is very abrupt. The enormous precipitation in the center of the island has resulted in the erosion of several deep canyons cutting into the table land. The writer visited one of these, the Olekele canyon, whose steep walls were clothed with luxuriant vegetation, including many liverworts and ferns. The most interesting plant noted was a begonia, *Hillebrandia sandwicensis*, the only member of the family known from Polynesia.

At the edge of the plateau is a fine open forest in which Metrosideros is the predominant tree; but as one penetrates to the center of the island, the moisture increases rapidly, and the ground becomes a bog, into which one sinks at every step. The carpet of mosses and herbaceous plants finally is replaced by an open bog with a few stunted shrubs and trees, and tussocks of coarse grasses and sedges.

Rock (35) has given a detailed account of the middle forest of Kauai, which is probably the richest in species of any in the whole Archipelago.

As we have already stated, the predominant tree of the marginal area is Metrosideros, with some *Acacia koa*, which belongs rather to the lower forest zone. Associated with Metrosideros are *Sideroxylon sandwicensis*, *Tetraplasandra waiemeae* and *Cryptocarya mannii*. Among other characteristic forms are species of Santalum, Elaeocarpus and Pittosporum.

Toward the interior of the plateau other trees become dominant, among them the Araliaceous genus Cheirodendron, and several Rubiaceae belonging to endemic genera, e.g., Kadua, Gouldia, and another endemic genus, Pelea (Rutaceae), most of whose species are restricted to Kauai. The ground in this region is saturated and the trees and shrubs are covered with a thick blanket of mosses and liverworts in great variety, and support many epiphytes, especially ferns. Among these are numerous beautiful filmy ferns (Hymenophyllaceae).

Besides the trees, many characteristic shrubs and herbaceous plants grow in this rain forest. Several endemic genera of Compositae, Dubautia, Raillardia, Wilkesia; two Liliaceae, Astelia and Dianella, also found in the Australasian regions, are common, but perhaps most notable of the plants of this region are the numerous species of Lobeliaceae, which reach an extraordinary development in the Hawaiian Islands. Unlike the low growing herbaceous species of the United States, some of the Hawaiian forms are 20–30 feet high, or occasionally more. These giant lobelias (Cyanea) have tall slender trunks with a crown of gigantic leaves, giving the plant something the aspect of a palm. The Lobeliaceae are especially abundant and varied in Kauai.

In the wet forests on all the larger islands, one may encounter one of the most remarkable of the Hawaiian plants, *Gunnera petaloidea*, which resembles a gigantic rhubarb, the huge peltate leaves being four or five feet in diameter.

The native palms of Hawaii all belong to the genus Pritchardia, with about ten species distributed throughout the islands, but not abundant as individuals.

Climbing plants are relatively scarce. The most conspicuous is *Freycinetia Arnotti* (Pandanaceae) which is very abundant and when in flower is rather showy, due to the red bracts of the inflorescence—but the most striking of the native climbers is the leguminous *Strongylodon lucidum*, with vivid scarlet flowers beloved of the honey-sucking birds.

There is, in general, a marked scarcity

of showy flowers among the native plants. Most conspicuous is the ubiquitous *Metrosideros polymorpha*, whose masses of crimson flowers are very showy. Some of the lobelias have rather attractive flowers, and occasionally a native Hibiscus with white, pink, or yellow flowers is encountered. Species of Cyrtandra and Scaevola, the former a genus abundant in the Malayan Islands, also have attractive flowers.

As in all volcanic islands ferns play an important rôle in the Hawaiian flora. They reach their maximum development in the rain-forest, where tree-ferns, (*Cibotium spp.*) reach a large size. While the majority of species belong to the great family Polypodiaceae, all of the families, except the Osmundaceae, are represented. In the rain-forest, often epiphytic upon the stems of tree-ferns, are several species of Hymenophyllum and Trichomanes. The curious *Ophioglossum pendulum* and the stately *Marattia Douglasii* represent the Ophioglossaceae and Marattiaceae.

In the dryer lowlands, *Gleichenia linearis*, a cosmopolitan species, forms impenetrable thickets, and on the recent lava flows ferns are among the earliest plants to gain a foothold. Among these the peculiar Hawaiian genus, Sadleria, is conspicuous.

The Upper Forest

Rock has made a special study of the upper forest on the lofty volcanoes of Maui and Hawaii. On Mauna Kea, in Hawaii, this forest reaches 11,500 feet elevation. It consists of four dominant species, the most abundant being *Sophora chrysophylla* and *Myoporum sandwicense*. With these in the lower areas are the ubiquitous Koa and Metrosideros. *Sophora chrysophylla* is one of the numerous Hawaiian species whose nearest relatives are found in New Zealand. The New Zealand species is so close to the Chilean *S. tetrapteris*, that it is by some botanists considered to be identical. Arborescent Compositae, *Raillardia arborescens* and *R. struthioloides* are an important element at the upper limits of the forest.

Bogs

The bogs found at elevations of 4,000–5,000 feet are characteristic features of the Hawaiian flora. Such bogs are found on the elevated plateaus of the older formations, as in Kauai, West Maui, and the Kohala mountains of Hawaii. The extensive bogs about Mt. Waialeale in Kauai afford excellent examples of such formations, which are reminiscent of the peat-bogs of the north temperate zone. The precipitation in Waialeale is enormous, approximating 500 inches annually, and the whole region is almost constantly covered with clouds.

The soil is saturated, and decayed vegetation may be found ten or fifteen feet below the surface. Sphagnum occurs in places, but for the most part the bog is covered with tussocks of coarse grasses and sedges. Two bunch-grasses—*Panicum monticola* and *P. isachnoides*—are abundant and in these tussocks two lycopods grow—*Selaginella deflexa* and *Lycopodium erubescens*. A most unexpected inhabitant of these bogs is a sundew, unknown elsewhere in the Islands, but apparently identical with *Drosera longifolia* of Northern Europe and America. Rock mentions among other characteristic plants a handsome blue violet and an orchid, *Habenaria holochila*, one of the four known orchids of Hawaii. Coarse sedges, including species of Carex, Rhynchospora and Oreobolus, are abundant. The latter is a genus characteristic of sub-antarctic America and New Zealand, and this is also the case with Astelia, a liliaceous genus. In this boggy region are a number of such temperate genera as Rubus, Vaccinium, Viola, Geranium. "Creeping forms of woody Metrosideros, Cyathodes, Geranium, Lysimachia, and a

number of rare, mostly single representatives of genera, which have their home in Antarctic (sic) regions of New Zealand, the Falkland Islands, and Southern Andes." (25, XXIV.)

Lava Flows

In all of the older regions volcanic activity has long since ceased, and the lava is more or less completely disintegrated. Hawaii, however, with its two great active craters, offers exceptional opportunity for studying the effects of the eruptions upon the vegetation, the invasion of the lava by various plants, and the establishment of new plant associations.

The frequent eruptions of Mauna Loa, with extensive lava flows down its slopes, sometimes reaching the sea, have resulted in the complete destruction of the vegetation over large areas.

Where the precipitation is light as on the lee side of Hawaii, the lava is little affected by exposure to the atmosphere, and much of the leeward or "Kona" side of the island is a desert of dead lava. Rock (35) mentions three lava flows in the Kahuku district which after an interval of fifty years showed no noticeable alteration.

Much the same conditions are found in the great crater of Haleakala, in Maui. Although there is no record of eruptions there is every evidence that activity ceased in relatively recent times, and the lava flows on the floor of the crater, protected by its lofty walls, show no signs of disintegration.

In the regions of heavy rainfall plants soon obtain a foothold on the lava and new soil is produced. It is probable that like the new flora of Krakatau (40), the first plants to settle on the lava are blue-green algae, and as in Krakatau, pteridophytes play an important rôle in the colonizing of the fresh volcanic soils. The writer in 1919 visited a great lava flow, which in 1881 threatened to destroy Hilo, the principal city of Hawaii. The great expanse of lava was easily recognizable, although it was covered with the beginnings of a new forest. Various pteridophytes were abundant, with a variety of ferns, among them the characteristic *Sadleria cyatheoides*, which seems to be one of the first to establish itself. Species of Lycopodium and Psilotium were also noted.

The most important element of the embryo forest was the ubiquitous *Metrosideros polymorpha*, which seems always to appear upon the recent lava. In the rain-forest this tree commonly begins its career as an epiphyte, especially on tree-ferns, where it often develops stilt-roots like those of so many species of Ficus.

Dr. H. L. Lyon, of Honolulu, who accompanied me on this occasion, informed me that practically all colonists on the new lava were strictly indigenous species. The introduced plants, such as the common weeds of this vicinity, failed to obtain a foothold.

Sometimes the forest on an elevation escapes the encroaching lava and forms more or less extensive islands in the surrounding lava flow. These islands, or "Kapukas" may give a clue to the vegetation which had occupied the region before the invasion of the lava. Rock gives an interesting description of one of these Kapukas, 56 acres in extent, near the great crater of Kilauea. "This little oasis shows no sign of lava rock but has rich, deep black soil which supports a marvelous mixture of vegetation. As many as forty species of trees are present in this beautiful park-like spot." It is gratifying to know that this is now included in the Volcano National Park.

When the writer first visited the volcano in 1892, the greater part of the road from

Hilo was through dense unspoiled rain-forest. In 1919 the lower forest, up to about 2,000 feet elevation had given way to cane-fields. Above this most of the forest along the volcano road had been cut down, or so ravaged by cattle and the consequent encroachments of Hilo grass and other weeds, that very little had survived. The last forlorn stragglers of the groves of tree-ferns that formerly lined the road were slowly dying, exposed to sun and wind, and skeletons of dead trees rose from a waste of tangled weeds and grass.

THE AFFINITIES OF THE HAWAIIAN FLORA

The remarkable richness of the flora, and the extraordinary degree of endemism has already been referred to, and this is especially true of the flowering plants.

Undoubtedly the aboriginal immigrants introduced a considerable number of plants that have become naturalized. The staple food plant, "taro" (*Calocasia antiquorum*) bread-fruit, banana and coconut probably all reached the country through human agency, and it is not unlikely that the Kukui (Aleurites) and Ohia (Jambosa), which now form forests all over the territory, may also have been thus introduced, as they are important economic plants found throughout Polynesia. Other species could be mentioned, e.g. *Cordia subcordata*, which are perhaps in the same category.

The botanist is at once struck with the preponderance of Old World genera among the trees and shrubs of the Hawaiian forest. The great majority which do not belong to endemic genera, are members of extra-American genera belonging to Australasia, or the East Indian regions. The commonest tree of the middle forest is *Metrosideros polymorpha*, a species found also in New Zealand, and throughout Polynesia. *Acacia Koa*, also extremely abundant, is of the phyllodineous type, especially characteristic of Australia. Pandanus and Freycinetia represent the exclusively Old World family Pandanaceae. The only genus of palms, Pritchardia, is confined to Polynesia. Other examples of familiar Old World genera are Pittosporum, Gardenia, Santalum and Dracaena.

Contrasted with these is the complete absence of any of the characteristic trees and shrubs of North America. Not only are there no conifers, but such universally distributed types as oaks, willows, poplars, maples, roses and a multitude of others, are conspicuous by their absence.

A marked feature of the Hawaiian flora is the complete absence of conifers, which are wanting throughout Polynesia. There are other forms which might be expected, but are either absent or very poorly represented. The wide spread genus Ficus is entirely wanting, and the important family Araceae has no certainly indigenous representatives. The scarcity of orchids is most remarkable. This, the largest family of flowering plants, with 17,000 species distributed over practically the whole world, is represented in Hawaii by but four species. There are no truly native Scitamineae, although species of Musa, Zingiber, Canna and Hedychium are completely naturalized.

Of the non-endemic genera, a few are cosmopolitan, like many grasses and sedges, Ranunculus, Lepidium, Silene, Geranium, Hibiscus; but the great majority belong to the South Pacific and the adjacent Malayan regions.

While Australia and New Zealand share with the Malayan region many genera and a good many species, there are certain genera, and even families, which are essentially Australian, and others which reach their maximum development in New Zealand. While Australia and New Zea-

land are often united as Australasia, they differ very much more in their floras than is generally supposed. In New Zealand especially, there is a considerable number of species which are closely related to, or identical with South American types. This "sub-antarctic" or "Fuegian" flora is also represented to some extent in the cooler and moister regions of Southeastern Australia, and has also some representatives in Hawaii. Examples of these are Astelia, Oreobolus, Nertera and Sophora. The latter has already been referred to. The geographical distribution of *Nertera depressa* is very remarkable. It is a pretty little trailing plant with scarlet berries, somewhat suggestive of the partridge berry (Mitchella), which belongs to the same family. Its range is along the Andes from Mexico to Tierra del Fuego, and it is common in New Zealand and Australia. It is reported also from the mountains of Tahiti. A similar, possibly identical species occurs in the higher mountains of the Malay Archipelago, as far north as the Philippines. The majority of the species are in New Zealand, which would appear to be the headquarters of the genus.

About fifty extra-American genera are common to Hawaii and the Australasian-Malayan region while the peculiarly American-Hawaiian genera number a scant half dozen (9).

An analysis of the Australasian flora, aside from the Fuegian element, shows two fairly distinct categories. In eastern and northeastern Australia and throughout New Zealand, the vegetation is markedly Malayan in type, and there is abundant evidence that both countries had former connections with the Malayan regions to the north, from which were derived, probably independently, many related or identical species. Some of these are shared with Hawaii, where such genera as Pandanus, Gardenia, Cyrtandra, may be considered as Malayan, rather than Australian.

The second element is the large and peculiar autochthonous flora of Australia, scantily represented elsewhere, and poorly developed in New Zealand. The latter, however, has a considerable number of dominant genera, some of them endemic, and a large proportion of endemic species.

Among the Hawaiian genera which have their greatest development in Australia are the following: Acacia, Byronia, Cassytha, Cyathodes, Dianella, Dodonaea, Exocarpus, Gahnia, Myoporum, Pseudomorus, Santalum, Scaevola, Vittadinia. In several of these, the majority of the species, outside Australia, are found in Hawaii. Scaevola is a good example of this. It belongs to the family Goodeniaceae which has many representatives in Australia but few elsewhere. According to Hillebrand (25), outside of Hawaii, which has eight endemic species, aside from the widespread *S. Lobelia*, only a single species, from New Caledonia, is known, while over fifty are found in Australia (12).

The relationships of the Hawaiian flora with that of New Zealand are very evident. The following characteristic New Zealand genera are well represented in Hawaii: Acaena, Astelia, Baumea, Coprosma, Gunnera, Metrosideros, Myrsine, Nertera, Oreobolus, Pittosporum, Sophora (*section* Edwardsia). Some of these, like Gunnera and Astelia, are shared with subantarctic South America. Coprosma, familiar to Californians through the extensively planted *C. Baueri*, is especially interesting, since of about forty known species, twenty-seven are found in New Zealand and nine in Hawaii.

Among the most remarkable plants of Hawaii is *Gunnera petaloidea*, already referred to, found in the wettest mountain

forests. Its gigantic leaves are much like those of the Chilean species sometimes seen in cultivation. The genus reaches its greatest development in the Andes and sub-antarctic South America and New Zealand. A single species occurs in the mountains of Java and in the Philippines, and it may be that the Hawaiian species is more nearly related to the Malayan species than to those of New Zealand.

As might be expected from the extreme isolation of Hawaii, not only is the proportion of endemic species very high, but there are many endemic genera as well. Some of these show more or less evident relationship with Australasian genera. The Hawaiian lobeliaceous Brighamia may be compared with the Australian Isotoma, Tetramalopium (Compositae) with Vittadinia, Pelea (Rutaceae) with Melicope, and Cheirodendron (Araliaceae) with the New Zealand Pseudopanax (25).

The Hawaiian Araliaceae are especially interesting, and show certain parallelisms with those of New Zealand. Of the five genera recognized by Hillebrand, three are endemic, and of the other two Reynoldsia is confined to Polynesia, and Tetraplasandra, with two endemic Hawaiian species, has a third species in New Guinea and the Sunda Islands. The endemic Hawaiian Cheirodendron is said to be close to the New Zealand Pseudopanax. Hawaii has four genera and fifteen species compared with six genera and seventeen species in New Zealand; while the whole United States has but three genera and eight species.

While the American element in the Hawaiian flora is much less evident than the types allied to those in the southern hemisphere, there are a good many species whose American relationships are unmistakable. These are mostly related to forms found on the American Pacific coast. The wild strawberry, *Fragaria Chilensis*, is identical with the American species, and the genus Sisyrynchium, except for the solitary Hawaiian species, is confined to America. Most of the very characteristic endemic genera of Compositae also have their nearest relations among the Western American types. Thus Campylotheca is close to Bidens and Coreopsis; Argyroxiphium, the "silver sword," and the closely allied Dubautia, are related to the Californian tar-weeds, Madieae, and the Hawaiian Raillardia is close to the Californian Raillardella.

A small number of other genera, e.g. Nama, Vallesia, are also apparently of American origin, but seem to be characteristic of South America rather than of Western North America.

Perhaps the most interesting family from the standpoint of evolution is the Lobeliaceae with over a hundred species. A small number of these are species of the cosmopolitan genus Lobelia, but the rest belong to five endemic genera of which the most important are Clermontia and Cyanea, and these show the most remarkable developments. Some of them assume tree-like dimensions, occasionally 30–40 feet in height. The slender trunk is often unbranched, and terminates in a palm-like crown of huge lanceolate leaves, beneath which are clusters of curious flowers.

Rock (36), who has made a special study of the family, states that nowhere except in South America, is the family so wonderfully developed. In South America the family is especially represented in the Andes and in Brazil. The extraordinary number of Hawaiian species is especially remarkable, as only four species are known in Polynesia, restricted to Tahiti and the neighboring islands of the Society group.

Pteridophytes

Hillebrand (25) lists 155 species of pteridophytes of which seventy-nine are endemic. As in all countries, a large majority of the species belong to the Polypodiaceae. The most primitive families, Marattiaceae and Ophioglossaceae, are represented by three species of Ophioglossum and one each of Marattia and Botrychium.

Ophioglossum pendulum is widespread through the Eastern tropics, and also occurs in southern Polynesia. The Hawaiian plants were smaller than specimens collected by the writer in Ceylon and Java, but otherwise identical. The single species of Botrychium is endemic, and Christensen (15) considers *Marattia Douglasii* as also truly endemic. A single species of Schizaea, *S. robusta*, also found in Tahiti, is the sole representative of the family Schizaeaceae. Five species of Trichomanes, three endemic, and four of Hymenophyllum, only one of which is known elsewhere, represent the filmy ferns, Hymenophyllaceae. One species, *Trichomanes parvulum*, whose tiny fronds are hardly half an inch in length, is found throughout the Eastern tropics, and also in the larger Polynesian islands.

Of the Gleicheniaceae, one species is endemic. The cosmopolitan *Gleichenia linearis* (*G. dichotoma*), is extremely abundant, and *G. longissima*, a common Asiatic and Malayan species, occurs in many parts of the islands.

The tree-ferns are all endemic species of Cibotium. *Marsilia villosa*, apparently most nearly related to the West American *M. vestita* is the only representative of the Hydropterides.

The widespread *Psilotum triquetrum* and *P. complanatum* are common, and Hillebrand lists ten species of Lycopodium, six endemic, and five of Selaginella, with three peculiar species.

Of the non-endemic species, aside from the cosmopolitan ones, the great majority are either Australasian or Malayan. The only American species, viz. *Asplenium fragile* and *Pellaea ternifolia*, are Andean species which reach Mexico and Texas.

A recent list of the Hawaiian Pteridophyta (15) lists 159 species, of which about 100 are considered to be endemic.

Bryophytes

Hepaticae

The writer has collected liverworts in Hawaii, where they are very abundant, especially in the wet mountain forests. Perhaps the most conspicuous and one of the commonest is *Dumortiera trichocephala*, a species occurring throughout the Indo-Malayan regions, but which is absent from the American tropics, where it is replaced by the cosmopolitan *D. hirsuta*, also found in Hawaii.

Often associated with Dumortiera is another conspicuous liverwort, *Wiesnerella denudata*, a monotypic species, known elsewhere only from Java, the Himalayas and Japan. Both of these characteristic Asiatic species inhabit wet shady localities, often on dripping rocks along streams. They would hardly seem to be adapted to dispersal over wide land areas, let alone such expanses of ocean as separate Hawaii and the Southern Pacific.

Other characteristic liverworts are the Anthocerotaceae, which are probably very old and primitive forms. They also are characteristic of the rain-forest. One genus, Dendroceros, is epiphytic, the plants of extreme delicacy. The thin-walled green spores germinate immediately on ripening, and would probably be quickly killed by even short exposure to

the heat and dryness of the open lowlands, and this probably is the case with most of the liverworts, so that it is scarcely likely that these could have been brought to the islands by wind or water transport (6).

Stephani's Index Hepaticarum (38) shows that aside from the endemic and cosmopolitan species, the Hawaiian liverworts are almost exclusively species belonging to Southern Polynesia, Australasia and Indo-Malaya. There are only two American species which do not also belong to the Old World.

The only likely means of transport for the spores of most species would seem to be in mud adhering to the feet of rapid flying migratory birds. As there are, at present, no migrants from the South Pacific, not to mention the great distance of the nearest source of supply, it is doubtful whether this will explain the presence of so many Asiatic and Australasian types. It is possible that some of the wide ranging sea birds might reach Hawaii from the Southern Pacific, but it is highly improbable that they would carry spores from plants living in the depths of the mountain forests.

In this connection we might note an interesting case. A Hawaiian liverwort, *Lepidozia sandwicensis*, is said to occur also in Alaska. The most common migratory bird of the islands, the golden plover, regularly migrates in large flocks from Alaska. It may well be that this bird was the means of carrying this liverwort to Alaska. As there are a number of other bird migrants from the Western American coast, it is highly probable that through these, such immigrants as the wild strawberry and other American types have reached Hawaii. As all the known migratory birds are American, they could hardly have played a rôle in the transportation of species from the South Seas.

From the data at hand, therefore, it is clear that the hepatic flora of Hawaii is closely related to that of the South Pacific regions, and southeastern Asia.

Mosses

From a recent list of the Hawaiian mosses (3) it is evident that much the same conditions exist as in the Hepaticae. The great majority are endemic, and where a species occurs outside Hawaii, it in nearly all cases belongs to the South Pacific or to the Malayan-Asiatic regions. An example of such distribution is *Thysanomitrium blumii*, which is found in Southern India, Ceylon, Sumatra, Java, Celebes, Borneo, Philippines, Formosa, Japan and Polynesia. More restricted in range is *Leucobryum hollianum*, recorded outside Hawaii only from Java and Borneo.

Algae and Fungi

The algae and fungi are too imperfectly known to afford an entirely satisfactory comparison with other regions. McCaughey has published a list of algae showing a good many cosmopolitan species, and a considerable proportion of endemics. Of the non-endemic, but not cosmopolitan species, the majority appear to be related to those of the South Pacific and Indian Ocean.

Stevens (39) has published an important list of the Hawaiian Fungi, but it is devoted mainly to parasitic forms. The larger fleshy fungi are still very imperfectly known.

As in the flowering plants, there is a high degree of endemism. Of one characteristic genus, Meliola, Stevens says, ". . . . all the Meliolas collected in Hawaii are found on plants indigenous to

the islands, and most of the host species are endemic with large representation of such typically Hawaiian genera as Gouldia, Clermontia, Kadua, Lobelia, Pelea, Scaevola, Straussia."

He recognizes the close relationships of these host plants with those of the South Seas, and concludes that the parasites must also have come from those regions. He thinks the Meliola flora is much older than the rust flora (Uredinales). "This relation of the Meliolas to the ancient flora of the islands clearly points to their long, even very ancient, association with these hosts or their progenitors."

Hillebrand, in the introduction to his Flora, considers at some length the problems of the origin of the Hawaiian plants. He was convinced that the archipelago has always been completely isolated, and that it has received all of its flora from outside. He believed that oceanic currents were the agents of transport, and especially the equatorial currents. He does not, however, explain how the seeds, spores, or fruits, of delicate forest plants, could have survived the long voyage from the South Seas to Hawaii.

This view of the complete isolation of the islands, from their first formation, was maintained for a long time, and the most comprehensive attempt to explain the origin and distribution of the flora on this theory, was offered by Guppy (24). His views as to the advent of the various elements of the flora are exceedingly ingenious and suggestive, but his conclusions cannot always be accepted without question.

Guppy believes that the islands first appeared above the ocean in early Tertiary time, and that the establishment of the vegetation followed the same course as that of the new flora of Krakatau after the great eruption of 1883. The conditions in the two cases are very different, however, although there is a certain apparent similarity.

Krakatau is less than fifty miles distant from Java and Sumatra, with their extremely rich and luxuriant vegetation, whence in less than twenty-five years, as the writer can testify from a visit in 1906 (7, 19), the devastated island was completely covered with abundant and varied plant growth. A comparison of Krakatau with Hawaii, over 2,000 miles away from the nearest mainland, and still more remote from the nearest habitat of most of its genera, is justifiable only to a very limited degree.

Guppy assumes that as in Krakatau the first immigrants were simple algae, mosses and ferns, carried by the wind. It is true that the spores of many ferns are well fitted for air transport, and the wide distribution of some species, like the common bracken fern, may be due to this. But some ferns, like Osmunda and the Hymenophyllaceae, are quite unfitted for wind transport over long distances, as their delicate green spores quickly lose their viability. It is hardly likely then that the filmy ferns of Hawaii could thus have reached the islands from New Zealand or the Malay Archipelago. The fact that nearly all the Hymenophyllaceae are endemic indicates that they belong to the ancient flora.

Guppy thinks the peculiar Compositae were among the earliest immigrants, antedating the influx of plants from the southern hemisphere which are now predominant. He recognizes the evident relationships with American types, and thinks they were transported by birds. This latter theory may be correct—but it probably was at a relatively late period, and not in the early Tertiary, as Guppy believes. At that time the highly special-

ized and relatively modern Compositae of California, e.g. Madia, Raillardella, could hardly have existed, and these are believed to be the nearest living relatives of the specialized Hawaiian Compositae. It seems much more likely that this composite element is relatively modern, and not a remnant of the primary flora. The geological history of California is such as to indicate that most of its numerous and peculiar Compositae are comparatively recent developments.

The Lobeliaceae are also regarded by Guppy as being, like the Compositae, of American origin, but this relationship is by no means so evident as in the case of the Compositae. The Lobeliaceae are also considered by Guppy to belong to the very early flora of Hawaii.

The predominant Malayan and Australasian types are thought to have come in at a later period. These plants Guppy believes were introduced through the agency of birds, especially fruit-eating pigeons. He assumes that at some former period there was a very active dispersal of plants in the Pacific Islands through birds, whose activity later, for some unexplained reason, ceased.

To believe that such plants as Gunnera, and many other inhabitants of the mountain rain-forests, could have been carried from New Zealand or Chile to Hawaii, is certainly a strain on the imagination.

Another difficulty in this connection is the present bird fauna of Hawaii. Aside from a number of American migratory shore birds and waterfowl, practically all the birds are peculiar to the islands, and the great majority belong to a single very specialized family, Drepanididae, whose relationships are problematical. Wallace (41) considers them most nearly related to the flower-peckers (Dicaeadae) of the Old World tropics. None of these birds could have been responsible for the introduction of the numerous South Pacific plants, and if these owe their introduction to bird agency, it seems strange that none of the birds responsible for these introductions should have left descendants in Hawaii. According to Guppy's hypothesis, these birds were fairly numerous, and not merely occasional stragglers, and it would be hard to explain the complete absence of such birds from the present fauna.

The strand flora of Hawaii is notably poor in species when compared with most tropical regions. The principal ocean drift at present is from the northeast, but the likelihood of many species from the Northern American coast, which might have drifted to Hawaii, becoming established in such a different climate, is not great. It is quite likely that such widespread species as *Ipomoea pes-caprae*, Scaevola, *Hibiscus tiliaceus*, may have been drifted to the islands from the south, as many strand plants have special adaptations for water transport.

It is quite likely that some species have been introduced through the agency of wind. This may be the case in some ferns, and it is not impossible that some of the Compositae may have thus reached Hawaii from Western America.

The small number of American types is remarkable inasmuch as there are agencies which might be expected to bring to the islands a good many plant immigrants. A considerable number of birds are regular migrants from the American coast, and the prevailing trade winds are from the same direction. Moreover, ocean currents frequently bring drift from Northwest American shores. None of these agencies, however, can account for the transfer of seeds from the remote regions to the south, whence it is certain most of the plant life of Hawaii has been derived.

While recognizing the difficulties in-

volved in attempting to explain the derivation of the existing Hawaiian flora, the evidence offered by the advocates of the theory of the strictly oceanic origin of the Archipelago is by no means adequate, as it involves assumptions, such as the extraordinary rôle of birds in seed-distribution, which are, to say the least, quite incapable of satisfactory proof.

The evidence for a former more or less direct connection with New Zealand, Australia and the Malay Archipelago, is fairly strong; and the admission of such communications will readily explain most of the difficulties involved in the theory that the Archipelago has always been completely isolated.

We may assume that the Hawaiian Archipelago, as it now exists, is but a remnant of a much larger land-mass which has been in subsidence for a long period, and that extensive subsidence has also occurred throughout Polynesia, and to a lesser degree in Australasia. One argument for this assumption is the great development of coral reefs in the Pacific, especially in Polynesia and northeastern Australia. The existence of active coral reefs involves continuous subsidence (17) and the absence of large land masses in mid-Pacific, with the innumerable small coral islands and reefs, can be explained most satisfactorily on the theory that the latter are the remnants of submerged land-masses of large size—possibly even of continental dimensions.

It is known that the Malay Archipelago was once united with the Asiatic mainland and that the southern extremity of the American continent was connected in some fashion with New Zealand. The remarkable similarity between the flora of Hawaii and these southern land-masses indicates, in the writer's judgment, that the present flora of Hawaii is in large part descended from types which were widely distributed over land areas which connected Hawaii with the ancient continents of the South Pacific. These ancestral types, in the course of ages, have become greatly altered in some cases, but others have persisted with little change. Presumably a good many forms have become extinct, and others have been introduced from outside since the isolation of the islands. In the latter category may probably be placed those Hawaiian species whose relations are evidently with those of the Pacific Coast of North America.

The objection has been brought against the continental theory of the Hawaiian Archipelago that certain types are absent, which on this theory we should expect to find. First in importance are such conifers as Araucaria, Agathis, and Podocarpus, characteristic genera of the Southern Pacific regions. Another notable case is the almost cosmopolitan genus Ficus. Another instance is the widespread family Araceae, with but two Hawaiian species, both almost certainly introduced by man. Other examples might be found, and these objections are valid ones, and not easy to explain.

The most probable explanation would be that some of these forms did exist, but have become extinct since the isolation of the islands. There are plenty of examples of plant extinction. We have but to recall the former wide distribution during the Tertiary of such now restricted genera as Sequoia, Taxodium or Liriodendron. Unfortunately there are no fossils to record the early history of the Hawaiian flora, and we can only conjecture what agencies may have caused the extinction of these missing types, supposing they did formerly exist. The most obvious explanation would be the extensive volcanic activity to which all the islands have been subjected, and whose destructive effects can be studied today in the

lava flows from Mauna Loa. Every region of the Archipelago has at some time been covered with lava, and it is not unreasonable to suppose that many species, especially those of local distribution, may have been destroyed as the direct result of volcanic eruptions.

An indirect result of the purely volcanic nature of the existing islands may have been a gradual extinction of species which require certain constituents absent from purely volcanic soils. The almost complete absence of granitic or calcareous soils, for example, might practically prevent the persistence of species present at an earlier period when areas existed which had not been covered by lava.

Another factor might also be considered, viz. the ravages of disease. Just as in large areas of the Eastern United States the chestnuts have been wiped out by the ravages of a fungus, so we may imagine species may have succumbed to similar enemies, and owing to the isolation of the Islands could not reestablish themselves.

We may conclude, then, that the bulk of the Hawaiian vegetation is made up of residual types, i.e. remnants of a flora common to the ancient much larger Hawaii, and the continental masses of the Southern Pacific and Malaysia. These ancient types have become more or less changed since the isolation of the Archipelago and their number has been augmented by a relatively small number of forms introduced from America subsequent to the isolation of the Islands.

FAUNA

The animals of Hawaii show the same predominant relationships with those of the South Pacific countries, only a small number of species indicating a derivation from American sources. This holds good for both vertebrate and invertebrate forms.

The subject of the land snails has already been referred to. Among the insects there is the same high degree of endemism, and the majority of species are related to Australasian and Indo-Malayan types (31).

In a former paper (9), the writer has given a statement of Professor W. K. Fisher of Stanford University, concerning some of the marine invertebrates of Hawaii. Professor Fisher says,

> In regard to the shallow-water and shore species of starfishes and holothurians which I have personally studied, the following general statement seems to apply: The starfishes are all tropical forms, and those which are not peculiar to the islands are chiefly Indo-Pacific, and comprise mostly wide-ranging species, some of which extend from the Red Sea to China and Japan, and thence to Australia. Considering the shallow-water species and those from moderate depths which are peculiar to the Hawaiian group, we find their nearest relatives in the Indian Ocean, East Indies, and north of Australia. In a few cases the same species from moderate depths, ranges into the East Indies as far as the Indian Ocean. Only one undoubted American starfish is found in Hawaii. There is no similarity in the faunas of the West Coast of America and the Hawaiian Islands.

The late Dr. D. S. Jordan also informed the writer that the shore fishes of Hawaii are related to those of the Southern Pacific and not to American types.

No indigenous Amphibia are known from Hawaii. This may possibly be explained by assuming that the islands were shut off at a period before that in which the modern amphibia, the toads and frogs, were developed. A similar condition obtains in New Zealand where only a single species is known.

About half a dozen lizards are known, all widespread species of the Southern Pacific region. It is probable that these were introduced with the early human immigrants or possibly may have reached the islands by drift.

With the exception of a single bat, the mammals probably all were introduced by human agencies.

Birds (33)

The birds of Hawaii are of extraordinary interest. Except for a comparatively small number of migratory species, wide-ranging sea birds and occasional stray visitors, all species are peculiar to the Archipelago. All of the passerine birds are endemic and mostly confined to the mountain forests.

Forty out of forty-nine species of passerine birds belong to a peculiar family, Drepanididae, confined to Hawaii, so specialized that their relationship with other birds is problematical. Wallace (41) thinks the family most nearly related to the flower-peckers, Dicaeadae, widely distributed through Australasia and the Old World tropics. Like the flower-peckers, their Hawaiian relatives are also flower visitors.

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ON THE SURVIVAL OF SPERMATOZOA IN THE FEMALE GENITAL TRACT OF THE BAT

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IT IS the current view that autumn constitutes the mating season of bats but that ovulation and fertilization are deferred until spring. By implication, the spermatozoa survive hibernation in the uterus (*Vespertilionidae*) or in the vagina (*Rhinolophidae*) where indeed they may be found at any time during the winter. This view Mr. W. Kenneth Cuyler and I have questioned (1927) on the basis of some years of observation on several species of Texas bats, studies which Mr. Cuyler expects some time to carry to a conclusion, as much material is already in hand. In the meantime, however, in connection with other studies on the mammalian reproductive cycle, the problem of the length of life of spermatozoa in general has forced itself upon my attention. I have, therefore, been over the entire literature again, which seemed all the more profitable in view of the publication of some important papers in recent years, notably those of Courrier, Nakano, and Redenz. Inasmuch as the significant literature is scattered and is without exception French or German, it seems worth while to review the topic for the benefit of others interested in the subject.

The problem began with Pagenstecher (1859) who found that on a certain January 23 the bat uterus was filled with sperms (*Vesperugo pipistrellus*), and that ovulation had not yet taken place. Van Beneden, however, finding spermatozoa about the ovaries and dividing tubal ova in December, January, and February, concluded that ovulation took place in the fall but that the ovum was arrested in its development, lying dormant until spring, a situation comparable to the arrest of development which Bischoff first described for the deer, Fries for the badger, and Patterson for the armadillo. It may be stated in passing that van Beneden has always stood alone in his interpretation. He was doubtless misled because he brought his subjects into the warm room, thus artificially ending their hibernation and speeding up the developmental process.

Three further authors (Benecke, Fries, and Eimer) published short but interesting papers in the second volume of the *Zoologischer Anzeiger* (1879). Benecke had access to several hundred specimens of *V. pipistrellus* and *Plecotus auritus* throughout the winter and uniformly found the uterus filled with a creamy mass containing active spermatozoa. The uterine tubes contained no sperms before spring. As early as December in one ovary or the other he found a graafian follicle already well enlarged, a point corroborated and emphasized by Courrier 50 years later. Benecke states that this follicle could be made to enlarge still more by keeping the bats in a warm place and feeding them; but he gives no details of such experiments. In the spring some sperms are said to travel up the oviduct; and the author makes the remarkable statement that he actually saw them through the thin wall of the tube. After fertilization the sperm mass is expelled.

Fries studied specimens of nearly a dozen species and clearly stated the case for the fall mating and the winter storage of spermatozoa. He recorded the new observation that the *Rhinolophidae* are exceptional in that in this family the female stores the sperm mass in the greatly distended vagina. He also studied the males and found their genital tracts swarming with live sperms and the accessory glands in a highly active state. The young born in the spring, he stated, are not mated in the fall but wait over until the following spring (*Vespertilio murinus*).

Eimer made a preliminary report in 1878, a more extended study (1879) after Fries's paper appeared. He kept individuals of *Vesperugo noctula* throughout the winter, examining the females from time to time and always with the same result: sperms in the uterus. The experiment was an excellent one and should be repeated and extended, as will be explained below, because Eimer failed to report the crucial point, namely, whether or not he kept males and females together.

These three authors were soon corroborated in all essential details by Vogt and by Robin in 1881. Robin stated that new copulations may take place on warm days of winter or during the early days of spring, a conclusion based upon actual observations on the horse-shoe bat (*R. ferrum-equinum*). Vogt thought that the tardy copulations of spring (horse-shoe and murine bats) concerned the virgin yearlings, for at this time one finds three kinds of individuals: (1) virgins with small graafian follicles and no sperms in the uterus; (2) females with uteri distended by a mass of sperms, mucosa edematous or seen detached in places; (3) females already ovulated. He agreed with Robin that the male remains fertile throughout winter for these supplementary matings.

Of the work thus far reviewed the embryologist Duval (1895) gave a rather complete account. He concluded that the adult females copulate but once a year, namely, in the fall, but the young females of the season wait over until spring and are impregnated then. Disagreements as to exact time of ovulation, gestation, and parturition he attributes to species differences. Duval observed three copulations on May 25, 1893, and gives a description of the act (p. 107). He also quotes Jobert (1872) who described parturition in the bat, which has been observed but two other times, namely, by Rollinat and Trouessart (1896) and by Sherman (1930).

That bats may also copulate in the spring was further asserted by Salvi (1902) and by van der Stricht (1909), although both base this conclusion upon their finding empty uteri in a small percentage of females in the early spring.

THE WORK OF ROLLINAT AND TROUESSART

In 1895 Rollinat and Trouessart also published two papers on the subject, covering collections made December 7 to January 15. These were preliminary to their extensive studies of 1896 and 1897, and confirmed the previous work and added several new points of interest. They discovered in the male a "bouchon urethral" or hard plug moulded to the wall of the urethra and persisting throughout hibernation. They presume the plug to consist of secretions from the accessory reproductive glands, especially the urethral gland of Robin (1881). Since in the *Rhinolophidae* the vagina is filled with the vaginal plug consisting of spermatozoa imbedded in firmly coagulated secretions of the male glands, Rollinat and Trouessart think that copulations during the winter are hardly possible, though Courrier (1924) suggests that the male with his os penis is quite capable of penetrating the vaginal plug. Rollinat and Trouessart marvel at

the astonishingly high degree of activity of the male glands throughout hibernation, which is such that the true rutting season would seem to be spring, as it is for most European mammals. In these preliminary papers the authors still interpret the continued activity of the male organs to serve the useful purpose of impregnating in the spring young virgin females born the preceding season. Like all their predecessors, Rollinat and Trouessart labor under the impression that spermatogenesis likewise continues in winter, a mistake only lately corrected by Courrier (1924) and by Nakano (1928).

In both their later papers (1896 on *V. murinus*, 1897 on *R. ferrum-equinum*) Rollinat and Trouessart, however, deny all matings for bats in winter or spring, holding, in other words, that the only rutting season is that of autumn. Contrary to their former opinion, therefore, they state positively that the virgin females born in June or July wait over until the fall of the succeeding year. They thus reverse their former opinion despite the fact that they, as well as others, actually witnessed copulation in the winter. They state, however, that a given female may copulate repeatedly in the fall, as evidenced by the increase in the size of the sperm mass as the season advances. The mass finally reaches a size much greater than any male could supply at a single ejaculation. The authors further postulate a sort of "Brown-Sequard" effect upon the male soma due to the resorption of sperms from the genital tract.

An interesting observation by these French workers concerns the leakage of spermatozoa into the bladder, whence they are evacuated with the urine, an observation which Nakano (1928) mistakenly believed he was the first to make. Rollinat and Trouessart significantly observed also that the bat population in caves, walls and belfries is not stationary but shifting. On warm evenings bats (especially *V. pipistrellus*) may frequently be seen flying about in the open. Males and females usually are found occupying separate quarters.

The authors describe a copulation and, in considerable detail, a parturition.

THE WORK OF GROSSER

The next study to be mentioned is a short one by Grosser (1903) recording what he calls a connective tissue atresia of the vagina. This seems a rather misleading title. What happens is that after copulation, which in *V. noctula* occurs soon after parturition in July, the proximal portion of the vagina not only undergoes the usual tremendous cornification of the vaginal epithelium, completely plugging the canal, but it also becomes denuded of epithelium because this sloughs off from the subjacent connective tissue. The plug remains as a cord in the vagina until expelled in the spring, when regeneration of the epithelium takes place. Assuming that further copulation is impossible to females in this condition, Grosser feels that his observation offers the best proof of the long survival of sperms for the eight months that the "atresia" lasts. It is quite clear, however, that what Grosser described agrees with Courrier's extensive findings, now to be mentioned, although Grosser is the only one yet to describe the complete denudation of the cornified layer in a given region of the vagina.

Grosser's short paper remained the single study undertaken on the sexual cycle of the bat by modern histological methods, although the broad facts had become common property by 1900. In 1895, however, Duval still complained that these facts had not yet become incorporated in the zoological textbooks of the day. It remained for Courrier (1924, 1927), student of Bouin, to work up the problems from the modern

viewpoint. Nakano (1928) published a histological study without being aware of either Courrier's work or those of Rollinat and Trouessart. Finally Redenz (1929) submitted the store of spermatozoa to experimental study with illuminating results.

THE WORK OF COURRIER

Courrier's two thorough studies go a long way towards establishing the prevailing idea of the long life of bat spermatozoa. He made excellent preparations of both female (1924) and male (1927) genitalia of a variety of bats, the most complete series being those of *V. pipistrellus*, *Miniopterus Schreibersii* and *V. serotinus*.

Among these *M. Schreibersii* was found to be exceptional for bats in that in this species copulation, ovulation, and fertilization occur in the fall, pregnancy ensuing at once and continuing during the winter. The male reproductive organs, the accessory glands as well as testes, undergo involution and remain in the "resting" stage or anoestrum until the next breeding season a year later. Neither the male nor the female retains a store of spermatozoa and the species thus conforms to other mammals having a single limited breeding season annually.

V. pipistrellus, on the other hand, is typical of bats. Its story is as follows: The summer months witness a regeneration of the spermatogenic tubules of the testes. After parturition and lactation copulation takes place and throughout winter the uteri remain filled with mucous masses laden with highly active spermatozoa. Courrier for the first time showed that the spermatogenic function rapidly ceases, a fact overlooked by Rollinat and Trouessart and their predecessors. The testes shrink, as does also later the head and body of the epididymis, while its tail hypertrophies greatly and harbors myriads of highly motile spermatozoa. The "follicular phase," however, continues in the female; and from the beginning of winter on one may recognize the follicle destined to rupture in the spring. As a result of this long continued follicular secretion, the vaginal mucosa proliferates until the lumen becomes completely obliterated by a veritable "bouchon vaginal," which is not, however, homologous with the vaginal plug that results from copulation in rodents and other forms, but consists, in the bat, entirely of epithelial cells from the vaginal wall, as first noted by Grosser (1903).

In the condition just described the males and females remain throughout winter. In the spring the plug is cast out and ovulation, fertilization, and pregnancy result.

In the *Rhinolophidae* the spermatozoa are retained, not in the uterus, but in a pocket on the ventral surface of the vagina at a point already indicated by a thin area in the epithelium in young virgin females.

In both the *Vespertilionidae* and the *Rhinolophidae* the accessory male reproductive organs remain highly active throughout winter, despite the degeneration of the spermatogenic tubules of the testes, while the interstitial tissue remains well developed. Hence the latter is made responsible for the endocrines which condition these secondary sex organs.

THE WORK OF NAKANO

From the work of Nakano (1928), who was investigating the glycogen of the genital tract, we learn that the Japanese *Vespertilio abramus* follows the same cyclic changes of the *Vespertilionidae* of Europe. He noted the reservoir of sperms in the cauda epididymidis of the male and in the uterus of the female. Glycogen appears in the uterine epithelium as well as in the tail of the epididymis shortly after sperms arrive in these organs. Glycogen in the

uterus is interpreted as of nutritive value to the spermatozoa, which may be correct if it can be shown that spermatozoa are ever capable of absorbing nutriment at all (*v.i.*). Nakano made the very significant discovery that the spermatozoa of the uterus were non-motile so long as they remained within the matrix in which they are imbedded. The observation was followed up by Redenz (1929) who contributed an illuminating experimental study.

THE WORK OF REDENZ

Redenz submitted fourteen females to examination. Two *Plecotus auritus* females were taken March 5 and 18 respectively while still in the torpor of hibernation. The former was the only female of the collection in which sperms were recovered from the uterine tubes. A mass of sperms was found in each of these two uteri. In most of the other specimens, which belonged to the species *V. murinus* and were captured April 11, 18, and 25, ova were found free in either the tube or the uterus. Sperms were recovered from the uterus in only two of these cases, the sperm masses having been expelled in all others. Most of the specimens, therefore, added little to the problem in hand; but the author presents for the first time some excellent photomicrographs of bat tubes containing ova in cleavage. The author's contribution to the physiology of the spermatozoa is more significant.

In going over the literature reviewed above one notes that former investigators uniformly reported the spermatozoa stored in the bat uterus in winter to be in a very active state. The reviewer has examined dozens of bats of several species by the same faulty technique and with the same result. Nakano (1928) and Redenz (1929) now find that the motility thus observed was due to the dilution of the sperm mass with the salt solution in which the specimens were examined. Without dilution the sperms are seen to remain absolutely motionless. If a fragment of the sperm mass is placed in Ringer's solution one may observe that the spermatozoa at the surface become more and more motile and gradually swim away; then those in deeper layers follow. At room temperature the motility lasts 16–20 hours, at the end of which time the sperms die. It is the function of the matrix containing the sperms to inhibit the motion so as to prolong their life.

In spring, then, according to the picture drawn by Redenz, ovulation occurs, the follicular fluid and other secretions descend into the uterus, and under their diluting or dissolving influence, "platoon after platoon of sperms" are "detailed off" to ascend the tube and seek the ovum awaiting their arrival.

FACTORS FAVORING THE SURVIVAL OF SPERMATOZOA

Such are the facts concerning the reproductive habits of bats so far as they have been ascertained to date. Are they sufficient to warrant the statement that the bat sperms survive in the female genital tract for from five to eight months? What is the answer in the light of comparative studies and in the absence of the direct experimental proof?

The first general condition favorable to the survival of the spermatozoa in the bat is its low body temperature. The animal is practically poikilothermous. Courrier found the mouth temperature to be 4° to 10°C., Redenz 14°. The latter is pretty near the temperature at which mammalian spermatozoa will live the longest in salt solution in vitro (cf. Hartman, 1932). Courrier found the rate of involution of the accessory sex glands of the male after castration to be extremely slow in winter, as also the rate of Wallerian degeneration

in several nerve tracts. Aron (1923) found similarly that castrated Tritons lost their secondary sex characters much more slowly in the cold than in the warm. In contrast to the condition in guinea pigs, in which, after castration, the spermatozoa of the epididymis die in 16 days, in bats they live for 60 days after castration (Courrier).

Parallel cases are to be found in fishes and Amphibia. Thus van Oordt (1928) states that the well known aquarium fish *Xiphophorus Helleri* may bring forth seven broods over a period of 10 months after a single mating. *Salamandra maculata* gives birth to young in May, whereupon a new batch of eggs are said to be fertilized from sperms stored in July (Gadow). There are also numerous cases in the invertebrates, as e.g. in the highly organized *Octopus vulgaris*, which, as Belonoschkin (1930) found, copulates from May to August. In the upper (secretory) third of the oviduct he found a sperm mass (non-motile until diluted) in which the sperms are said to survive until the following spring.

The second factor favorable to the longevity of the ripe spermatozoa is their immobility brought about by the medium in which they are placed. This immobility in the bat, discovered by Nakano and confirmed by Redenz, is, however, but illustrative of the general law that spermatozoa are endowed with a limited supply of energy and when this is used up they die. Wherever spermatozoa are stored there is a provision for the inhibition of their movement. They are motionless in the testis of the sea-urchin but when dispersed in sea water they become instantly highly motile. Sperms are inhibited in the mammalian testes but when ejaculated become motile and in the female genital tract are short-lived because of their high degree of activity. It is improbable that ripe spermatozoa are capable of absorbing any nutriment from the surrounding medium.

A further pursuance of this question is, however, out of place here. The reader is referred to the chapter on "Mass Physiology of Spermatozoa" in Allee's *Animal Aggregations*, 1931.

DO BATS COPULATE IN SPRING?

The facts thus far reviewed point to the reasonableness of the current interpretation of the breeding habit of most bats, namely, that the spermatozoa which the female receives in one or several matings in the fall (August to October according to species) live until spring and are the identical ones which function in fertilization at the end of this period. Yet it must be remembered that the conclusion is entirely inferential, for no one has yet, as already indicated, kept isolated females from fall to spring and seen them pregnant at the end of the hibernation. Eimer's experiment in this direction is incomplete in several respects. The alternative theory, namely, that bats copulate during warm spells in winter and again in the spring just before the time to ovulate, has arguments in its favor. Robin, Vogt, Duval, and Rollinat indeed, witnessed matings in these seasons and van Beneden secured eggs in cleavage from bats in the winter months. It is, therefore, certain that just as soon as female bats are subjected to warmth they are ready to copulate and, given sufficient time, to ovulate and conceive. As to the segregation of the sexes during hibernation, which seems to be the rule, Rollinat and Trouessart speak of the bat populations of crevices and caves shifting their position from time to time throughout winter and in mild weather fluttering out in the open. It should also be pointed out that in those species that mate in July and August, the store of spermatozoa may be subjected to elevated temperatures which sometimes

prevail in September before the winter sleep comes over the animals.

Whatever view one is inclined to accept on the present problem the temptation is great to become teleological and ask: if autumn marks the real mating period, why the colossal storage of sperms in the tail of the epididymis and why the continued hypertrophy of the accessory sex glands of the male? The most likely answer one can make is that, contrary to the opinion of Rollinat and Trouessart, the males are still in a condition to impregnate the young females of the previous year. It seems rather wasteful, however, that all the males should reserve their potency and fertility for the benefit of the debutantes of spring not yet mature at the last harvest season.

The chief consideration, however, that leads to a questioning of the current interpretation of the bat cycle is the fact that in those species in which the male is free of sperms in winter the female is likewise free of sperms. The case of *Miniopterus Schreibersii* has already been noted. In this species copulation, ovulation, fertilization are closely connected events. The male performs his procreative function, whereupon his organs atrophy until the next year. A similar case is that of *Nyctinomus mexicanus* of Texas, whose breeding season Mr. Cuyler and the reviewer found to occur only in spring. There is the same opportunity for mating as in other species of the same locality that do mate; but in *Nyctinomus* the organs of both sexes are in the resting stage in which they remain until spring. Perhaps these cases are the more primitive, conforming as they do to the habits of mammals in general; the more typical cheiropteran behavior might, therefore, be thought of as developing secondarily. The latter is peculiar in several other respects. Whereas in rodents mating ensues immediately after parturition, in bats it follows weaning of the young. Mating moreover occurs in the absence of ripe follicles. In other respects bats are still to be brought into the picture of what we conceive to be typically mammalian reproductive behavior.

SUMMARY

Typically, bats mate in autumn after the female has weaned her young, at which time the post partum involution of her organs is complete and a new sexual cycle may be said to have begun. In the male spermatogenesis has passed its zenith and the testis has begun involuting; but the epididymis, especially the tail, is greatly distended with sperms, while the accessory glands (prostate, seminal vesicle, urethral gland of Robin) are enlarged and highly secretory. This condition is maintained with greater or less diminution until spring. Involution of the male organs occurs while the female is pregnant but regeneration follows promptly in summer. Oestrus in the female (follicular phase) continues from fall until spring or six to eight months; hence pregnancy and lactation alone interrupt her oestrus and she may be said to have no anoestrum. The male has but a short anoestrum (March to July), for his sexual vigor and fertilizing capacity is maintained by interstitial tissue (Courrier) from July to March, even though during the larger portion of this time spermatogenesis is in abeyance.

Two exceptions to this rule are known: (1) *Miniopterus* which breeds only in fall; here anoestrum lasts in the male from October to July (Courrier); (2) *Nyctinomus*, which breeds in the spring and here anoestrum lasts from May to March (Cuyler and Hartman). The California mastiff bat may also belong to this class (Howell, 1920). Since this represents the ordinary mammalian condition it probably consti-

tutes a remnant of the primitive cheiropteran condition.

The mass of spermatozoa typically found in the female genital tract at any time in the winter is, according to the current view, supposed to survive hibernation (6–8 months) and remains available for fertilization in the spring. For such survival the lowered body temperature of the poikilothermous bat (10°–14°C.) and the mechanism for immobilization of the sperm in a coagulum constitute extremely favorable conditions. Nevertheless it is the purpose of this paper to point out that the proof has not yet been forthcoming finally to establish the view that the sperms ejaculated in the fall are the ones that will fertilize the ovum in the spring. Observed winter and spring copulations speak in favor of repeated copulations in these seasons. The crucial experiment, which is quite feasible and has already been partly carried out by Eimer, consists of capturing females in the fall, keeping them isolated from males throughout winter and observing whether or not a pregnancy ensues at the end of hibernation.

Regardless, however, of the outcome of such an experiment on the female, the long life of spermatozoa in the epididymis of the male is undoubted, for both Courrier and Nakano have demonstrated the cessation of spermatogenesis as long as seven months prior to the final disappearance of the last summer's crop of spermatozoa from the tail of the epididymis.

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SEX PROBLEMS IN HEMP

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ALTHOUGH sex has been recognized in animals since before the time of recorded history the recognition of sex in plants is, with few exceptions, less than 250 years old. In Mesopotamia and in Egypt, where the date palm has been cultivated for ages, the distinction of male and female palms has been made for at least 4000 years as shown by inscriptions describing and illustrating the manner of pollinating the female flower clusters by racemes of male blossoms, in practically the same way as that still used by the Arabs and Egyptians. The earlier herbalists ascribed sex to various plants. Thus one kind of fern was called Male Fern and another Female or Lady Fern, and one kind of Dogwood was named *Cornus mas* and another *C. foemina*. These differences, however, were specific or even generic and had nothing to do with the sex of the plants.

The failure to distinguish sex in plants is due to the fact that in the popular mind sex distinction is associated with distinction of *individuals* of different sex, as in the domestic animals and in man. In Europe hemp and the hop were the only commonly cultivated plants in which the plants are dioecious. Here the pollination is accomplished by air currents and there is nothing similar to the sexual processes in animals. The remainder of the commonly cultivated plants possessed perfect flowers and in some of them, wheat, barley, oats, pea and bean, are usually pollenized *before* the flower had opened. Thus the necessity for sex was not recognized.

Nehemiah Grew in 1682 indicated the stamens as male organs and the pistils as female organs, from morphological reasons only. Camerarius in 1694 was the first investigator to report the results of actual experiments by which he proved the correctness of Grew's assumptions. He excluded pollen from the pistils of *Mercurialis*, *Morus*, *Zea mays* and other plants and obtained no seeds except when he applied pollen from the male flower of the same species. The publication of the results of these experiments was followed by numerous experiments both in Europe and in America which confirmed the sexual nature of stamens and pistils and led soon to successful attempts at hybridizing various kinds of plants.

Hemp, *Cannabis sativa*, is a native of Asia and has been cultivated both for its fibre and for the drug "hashish" which is in great demand in Central Asia, Persia, Afghanistan and Northwestern India. Its culture as a fibre plant has spread all over the temperate regions of the world and it has escaped and become a weed of low lands in various places. Thus it is very abundant along the Missouri River and tributary streams in Eastern Nebraska and Western Iowa.

The plant as grown for fibre is 8 to 12 feet or more tall while the varieties grown for the drug are usually only about 3 to 4 feet tall. The male plants are usually more slender than the female plants, sometimes slightly paler green, and have but few and small leaves at the top. The clusters of male flowers are large and conspicuous. As soon as the pollen has all been

shed the plants die, long before the female plants. The latter are usually stouter and leafy to the apex, the flower clusters being smaller and less conspicuous (before the seeds begin to form). The female plants have a strong, somewhat pungent ódor, especially after the seeds are beginning to form.

Normally, when sown in the summer time, about 45 to 47 per cent of the plants that grow to maturity will be males, but the ratio may vary considerably in adjacent plats from the same lot of seed. Sometimes up to 55 per cent will be males. Usually the male plants will have no female flowers but a small percentage of the female plants will develop, as they grow older, a few male flowers. In 1926 or 1927 the writer found a plant, resembling a male plant in habit, with perfect flowers, the pistil and stamens apparently being functional. The flowers did not develop until just before an early frost which destroyed the plant.

THE EFFECT OF AGE OF POLLEN

Perhaps the first systematic experiments to determine the factors involved in the determination of sex in any plant were those begun by Dr. Theophilus Ciesielski in 1871 in Poland. These experiments covered a series of eight or ten years or possibly longer, but were not reported until 1911. The earlier experiments had to do with the effect of close or distant planting, with only negative results. Planting at different phases of the moon also was without effect upon the sex ratio. Growing the plants in light and in shade, in moist and in dry soil, and in rich and in poor soil were also equally ineffective. The ratio remained about the same; 40 to 50 per cent of the plants were males, the remainder females. Similar result were obtained whether the pollen was taken from the top, middle or lower portion of the inflorescence. The only definite results were those where the pollen used was of different ages.

In the male hemp plant the stamens usually begin to dehisce a little while after sunrise when the atmosphere begins to become drier. These flowers were collected early in the morning shortly before the stamens opened and the pollen from some of these was scattered on the flowers of female plants placed indoors or at a considerable distance to prevent chance pollination. Some of the male flowers collected at sunrise were kept until sunset and were then used to pollenize other female flowers. With slight variations as to details these experiments were repeated several years. The seeds were saved and planted out-of-doors next summer. From the flowers pollenized with freshly produced pollen the seeds gave 85 to 90 per cent male plants while the seeds from flowers pollinated with 12 hour old pollen gave 90 to 100 per cent female plants. Ciesielski emphasizes the fact that he repeated these experiments several successive years, always with the same results. He concludes, therefore, that there is a tendency toward maleness in fresh pollen and that as the pollen becomes old this tendency changes from maleness to femaleness.

In 1921 Lilienfeld reported the results of experiments performed by him to test the correctness of Ciesielski's conclusions. He could not find any differences in the sex ratio whether the pollen used was fresh or 12, 30 or 36 hours old.

Ignorant of Lilienfeld's work the writer began experiments along the same line a short time later. This work was carried out in the greenhouse at first and then out of doors. The number of seeds obtained in the greenhouse experiments was too small to enable any definite conclusions to be drawn. Out of doors the female inflor-

escences were bagged and allowed to remain covered one or two weeks. Then the bags were temporarily removed and all flowers whose ovaries had started to enlarge (indicating pollination before bagging) were removed. Then the flowers were pollenized with pollen of the desired age and again covered until the male plants were all removed a few days later. Pollination was accomplished in various ways. For fresh pollen in most cases anthers were selected that were just opening and the pollen dusted from these on the female flowers. Sometimes unopened anthers were torn open and the contents applied to the stigma. The flowers were then rebagged. For older pollen, clusters of male flowers on the point of opening were bagged early in the morning after removal of all previously opened flowers. Since nearly all of the male flowers open at about the same time the pollen in the bag will be approximately of equal age when the bag is removed from the inflorescence. Such bags of pollen were held various lengths of time. When it was desired to use pollen of any given age the corresponding bag of pollen was placed on a female influorescence that had been bagged as described above, and shaken and beaten until all the flowers were pollinated. This bag was allowed to remain or a fresh bag was placed over the inflorescence until all bags were removed after the destruction of all male plants. Pollen used in these series of experiments was fresh, 8–9 hour, 14–16 hour, 24 hour, 42 hour and 64 hour pollen.

The seeds resulting from these pollinations were planted next year and the ratios of male and female plants determined when they began flowering. The plants grown in 1926 from pollinations made in 1925 gave for "fresh" pollen 44.2 per cent male plants, the control from open pollinated seeds from other branches of the same parent plants giving 49.3 per cent males. The seeds produced from "old" pollen gave 43.4 per cent male plants and their controls 48.7 per cent males. In 1927 the figures for seeds resulting from 1926 pollinations were 47.2 per cent males for "fresh" pollen, 53.5 per cent males for 10 to 12 hour old pollen, and 47.1 per cent males from pollen 17–27 hours old. The controls were respectively 53.5 per cent, 49.9 per cent and 50 per cent males. Although the figures showed considerable variations it is clear that they agree rather closely with those obtained by Lilienfeld and do not give any support to Ciesielski's reports. Either the latter failed to make accurate experiments or the variety of hemp used by him responded in an entirely different manner from the varieties used by Lilienfeld or the writer.

THE EFFECT OF MUTILATION

The sex question in hemp had already been attacked from another angle by Pritchard in the years 1909–1914. This investigator removed the flowers and flower buds and even leaves and portions of the tops from various hemp plants of both sexes. Omitting the earlier experiments in which the numbers involved were few the results of his 1913 mutilations may be considered. Fourteen male plants which bore no female flowers had all their flowers and flower buds removed. Eleven of these produced only male flowers on their new growth but on two of the plants a few sex-intergrade flowers and female flowers appeared among the male flowers (four female flowers to 7390 male flowers) and one produced all (461) female or intersex flowers. Of the 31 female plants that had their flowers removed four had at the time a few male blossoms, a total of 1016 male to 29,950 female flowers, or a little over 3 per cent. After new growth took place these four plants gave 17,137 male

blossoms and 18,861 female blossoms, or almost 48 per cent male plants. The twenty-seven female plants that had no male blossoms at first had on their new growth 160,862 flowers of which 24,242 were male (or intersex) flowers, approximately 15 per cent.

In connection with the foregoing effects of mutilation upon the sex ratio in hemp may be noted the report of J. E. Higgins upon *Carica papaya*, in which sex changes have been brought about in a similar manner. This herbaceous tree, if it may so be called, is normally dioecious although trees with hermaphroditic flowers are not rare. Upon cutting back a male tree it frequently happens that the new shoots produce female flowers or hermaphroditic flowers, but Higgins could not induce female trees to change their sex by cutting them back.

SEX CHROMOSOMES

The discovery of chromosome differences in the two sexes of certain insects thirty years ago, followed by the realization that this is a very general condition throughout most of the animal groups, led to investigations to determine whether similar conditions held in those plants in which the sexes are separate. The earlier studies by Strasburger gave negative results but in 1917 C. E. Allen reported sex chromosomes in *Sphaerocarpus*, one of the Hepaticae. Six years later they were reported in a number of Dicotyledons and in one Monocotyledon. Among the former was the hop (*Humulus lupulus*), a near relative of hemp. In the next year, 1924, Hirata, a Japanese investigator, found both X and Y chromosomes in one variety of hemp. The male plants were heterozygous with 18 autosomes + X + Y and the female plants homozygous, 18 + X + X. The male gametes were of two kinds, with either X or Y chromosomes + 9 autosomes. The female gametes all had 9 autosomes + X. In another variety the two could not be distinguished by size and shape. McPhee in the same year reported his investigations in which the variety of hemp studied did not show distinguishable differences between X and Y chromosomes.

THE EFFECT OF LIGHT

In the meantime Dr. J. H. Schaffner had been carrying on studies on the sexual expression in hemp and other dioecious and monoecious plants. Planting hemp seeds in December he obtained approximately equal numbers of plants that had the aspects respectively of male and female plants. However, 88 per cent of the female plants produced some intersex flowers or some purely male flowers and 84 per cent of the male plants produced some intersex flowers or female flowers. These plants were the descendents from two generations of plants that when grown in the summer were pure male or female with no intersexes. Only a few of the flowers showed complete sex reversal, most of them being intermediate, with malformed and nonfunctional stamens and pistils or organs showing the characters of both, e.g. stamens bearing stigmas, or pistils with microsporangia. The few complete reversals consisted of normal male flowers producing functional pollen on the female plants and, much more rarely, normal female flowers on male plants. This author is very emphatic in his conclusions that the sexual differentiation is not explicable by a "Mendelian hypothesis of sex" but is the result of environmental factors. The particular factor involved in the experiments just described was the "abnormal environment, mainly a lack of light." The author carried out further experiments which led him to conclude that not merely shortened daylight but also reduced fertility

of the soil increased the tendency toward sex-intermediacy or sex reversal.

McPhee repeated some of these experiments with several different strains of hemp, using chambers which could be closed at different times of day so that the plants could all be grown during the summer and yet have different daylight periods. Although he did not obtain such striking percentages of change as Dr. Schaffner did he found that with the shortening of the daylight the percentage of intersex flowers was increased, although the plants retained their general aspect of male or female plants. He was successful in obtaining a few viable seeds from female flowers produced on male plants and pollenized by pollen from the same plants. Only four such seeds produced plants that grew to flowering. Of these three were male plants and one female. On the other hand many more seeds were obtained from flowers on female plants pollenized by pollen from male flowers on the same plant. Out of 161 such plants grown to flowering, 158 were typical female plants. The three male plants are believed by McPhee to have been due to accidental pollination from male plants. Flowers on these female plants were pollinated from male flowers produced on the same plants under the influence of shortened daylight and from these a few second generation plants were obtained, like their parents all female. Apparently the condition of femaleness is a matter of heredity.

McPhee found that there was great difference in the ability of various strains of hemp to be affected in the sex ratio by different lengths of daylight. Some strains appeared to be entirely unaffected by such treatment and produced pure males or pure females, regardless of the shortening of the daylight period. Other strains were very readily modified by the same treatment.

DISCUSSION

When we bring together the various observations with reference to the sexual conditions in hemp we find a number of apparently contradictory conditions. In at least one variety of hemp Hirata has demonstrated the presence of distinguishable X and Y chromosomes, the male plant being heterozygous and the female homozygous. In other varieties these chromosomes are not distinguishable but it can hardly be doubted that they are there even though alike in appearance. The plants grown from seed whether in summer daylight length or in shortened light periods are in about equal numbers, male and female, so far as the vegetative characters are concerned. Yet by cutting back the plants and growing them in shortened light periods Schaffner caused such plants to show partial or in a few cases complete sex reversal. From these series of observations Schaffner is very positive in his conclusions that the heterozygous and homozygous chromosome condition has nothing to do with the determination of sex in hemp. From his studies in other dioecious plants he is even more firmly convinced of this fact. McPhee, noting that the male or female aspect of the plant is fixed from the beginning regardless of the environment, believes that the sex is determined in a Mendelian manner, but that the sexual expression may be modified by environment. The fact that seeds from female plants pollenized by pollen produced, under the influence of the environment, on the same plants give rise only to female plants would seem to substantiate the idea that the chromosome condition is the determiner for sex.

Hirata suggests that the Y chromosome has a tendency toward maleness, the X chromosome a tendency toward femaleness. The male tendency in Y over-

balances the female tendency in X so that a plant heterozygous for X and Y is normally male and an XX plant is normally female. In the autosomes the sexual tendencies are about equally balanced. The sexual determination is brought about by the excess respectively of the enzyme "andrase" for the male or of the enzyme "gynase" for the female. Under abnormal environment or under the influence of mutilation the dominant enzyme formation may be partially suppressed, allowing the opposite sex to express itself partially (intersexuality) or completely (sex reversal).

The writer believes that both views may be reconciled in the following manner. The sexual expressions as male or female are the result of different metabolic rates in the individual, as Riddle has suggested for the pigeon. A marked change in this metabolic rate from a higher to a lower rate or the reverse will change the expression of sex. If the change is to an intermediate metabolic rate the result will be the production of intersex forms. Under normal environmental conditions the determiners for the higher or lower metabolic rate are the sex chromosomes, hence the usual approximately equal numbers of males and females. Since this chromosome condition exists from the fertilization of the egg the embryo in the seed is already predetermined for a certain metabolic rate, i.e. for a definite sex. Hence we find that the plant will have the vegetative characters of a male plant or of a female plant from the beginning. If the external environment (light, moisture, etc.) is normal the plants will produce male or female flowers, respectively. Extensive mutilation will affect the metabolic rate, as will shortened daylight, infertile soil, etc. Depending upon the degree of this alteration there will be produced a few or many intersex flowers or even a complete sex reversal.

Sex reversal has been brought about by Schaffner in *Arisaema triphyllum* by simply transplanting the corms of male plants from poor, dry soil to rich, moist soil, or of female plants from rich, moist soil to poor, dry soil. An intermediate type of soil may produce monoecious plants with both male and female flowers in the same spathe. Hemp, *Arisaema* and *Carica* and other plants in which sex changes have been reported as a result of changes in environment or of mutilations are species which are as it were only sporadically dioecious in families or orders in which the normal condition is hermaphroditism or monoecism. Most of the Urticaceae (in the wide sense) are either monoecious or hermaphroditic. Even in *Carica papaya* perfect flowers are not rare and the nearly related plants (e.g. Passifloraceae) are hermaphroditic. Clearly sexual differentiation of the plants into male and female plants is not an ancient or very deep seated character. This is quite in contrast to the sexual condition in animals which is very ancient and deep seated. Even in the family Salicaceae we find intersexuality. Probably there are no families of flowering plants where the distribution of sexes in different individuals is deep enough to prevent partial reversal by environmental changes.

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LIGHT AND SEXUAL CYCLES IN STARLINGS AND FERRETS

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DURING the years, 1926–28, at Trinity College, Hartford, the writer, with Morton H. Chapnick (1, 2, 3), studied and described the normal sexual cycle of male European starlings (*Sturnus vulgaris*) from birds killed at approximately fortnightly intervals and checked this study by repeating for a second year. An attempt was made to correlate the observed changes in the testes with environmental factors such as temperature, barometric pressure, and daily hours of daylight. With the equipment available, it was impossible to measure variations in light intensity over these periods or to follow changes in type and quantity of food consumed by the birds. Of all the environmental variables tested or ascertained in connection with this study, daily hours of daylight increase and decrease uniformly each year, so that the same dates in successive years have similar periods of daily daylight, though intensities vary from year to year. The conditions of the testes of the birds underwent changes which were surprisingly similar in the two years studied. Temperature and barometric pressure varied very irregularly and the testis changes appeared to bear no consistent relation to either of them.

The writer therefore proceeded to an experimental study of the possible relation of the ebb and flow of the tides of testis activity to the waxing and waning of daily light periods.

About this time, Professor Wm. Rowan (4), of the University of Alberta, Canada, working with Juncos, showed that seasonal migrations of those birds were correlated with the seasonal changes in the sexual conditions of the birds and these in turn with the daily hours of daylight to which the birds were exposed. His experiments led to the conclusions that the birds migrate if their sex glands are either increasing or decreasing in size and activity; but that they fail to do so if the sex glands are at either their maximum or minimum phases of the sexual cycle. He is continuing with his investigations of the problem of this relation of migration to sexual cycles and to seasonal variations in duration of day, using changes in daily period of illumination as his modifying factors.

IS LIGHT OR EXERCISE THE CONTROLLING FACTOR?

Owing to some experimental results obtained with a few birds during the spring migration period, subjected to enforced exercise for considerable periods after dark, without increased light periods, he concluded that it is not the increase of daily periods of light, as such, that induces increased sexual activity in the birds in spring; but the longer periods of muscular exercise daily, permitted by the lengthening days, that leads directly to the spring increase in germ-cell or sexual activity of the Juncos (4, 5).

In beginning the experiments on star-

lings, Professor Rowan's hypothesis as to the cause of changes in the sex glands was taken as a working hypothesis, though it did not seem to be proved beyond question that exercise was the factor really concerned, instead of light as radiant energy. His conclusions did not seem to be the only ones compatible with his data. Alternative explanations were therefore tested. Apparatus modelled after his, with alterations to increase its effectiveness, was used to cause the birds to be disturbed from their roosts every 20 seconds, for definite periods after nightfall. By testing the effects of 6–7 hour periods of this added work against those of equal periods of electric light from 60 watt bulbs and against controls, without added work or light, it was found that, in the months from December to April inclusive, added light was a very potent agent in inducing sex-gland activity, including spermatogenesis, in the starling. On the other hand, added work periods without added light were not only not effective in inducing spermatogenic activity, but tended to reduce both the size of the testes and their germ-cell activity.

However, by modifying the experimental method and the previous condition of the birds used, it was found that increased exercise periods led to a lag in onset of light-induced changes in the testes, whether those changes consisted of increase of activity induced by increased light exposure, or of decrease of activity induced by decreased daily exposure to light. This lag in onset was usually more than made up for later, by increased acceleration of the testis changes, induced by changes in exposure to light.

Light exposures after sundown, up to 6–7 hours per night, led to complete spermatogenesis and maximum testis size in 4–6 weeks at any time from December to April, while controls, kept on daily light periods similar to those of winter in duration, did not come into activity even in April, May, or June, when, in nature, the testes are at their maximum of activity and size. The testes of birds on forced exercise periods added to short or winter-length daily light periods, became smaller in size and less active in spermatogenesis than those of controls without either added light or exercise periods. The state of activity of the testes (and of ovaries, as judged by gross inspection) could be modified at will, in either direction, within the limits of the natural changes, by increasing or decreasing the daily periods of illumination. Birds could also be kept, for a month or more, in a condition of partial regression, by holding constant the daily periods of illumination and exercise (7).

THE EFFECT OF WAVE-LENGTH

Further studies, in 1928–1931 (8, 9, 10, 11, 12), with aid from the Committee for Research in Problems of Sex of the U. S. National Research Council, showed that the degree of stimulation of testis activity varies with the intensity of the illumination used and depends also on the color or wave-length of the light. Red was found to be highly stimulating, while green of the same luminous intensity was not stimulating but somewhat inhibitory to testis activity and to that of ovaries. Violet light, of low luminous intensity, was apparently slightly inhibitory as compared with lack of illumination, within the limits of the experiment.

Daily period, intensity, and wave-length of light reaching the birds were factors in controlling the seasonal sexual cycle in starlings, when the diet was kept adequate, varied, and rich in vitamines, proteins, fats, and carbohydrates. No mating nor egg-laying was observed in any of these experiments, even in birds brought to com-

plete sexual maturity, as judged by histological examination. These reactions seem to be controlled by factors outside the conditions operating in these experiments, and not by those inducing complete gametogenic fitness for breeding, if this fitness is judged from histological conditions alone.

Experiments also indicated that the maximum effect and consistency of results were to be obtained by large and immediate increases in periods of illumination to a maximum, rather than by gradually increasing periods. Filtered red light of 1.7 foot candles luminous intensity, acting for 6 hours per night after a 9½ hour daily daylight period in a basement room, induced approximately complete spermatogenesis in 23 days, in December and January. Green light of equal intensity caused slight regression even from the normal mid-winter quiescent state, in a great majority of cases.

In the study of the normal sexual cycle of these birds (3), it was noted that regression of the testes invariably set in before June 15, while the daily periods of illumination were still increasing in duration and intensity. Experimental analysis indicated that with red light, or even with artificial midsummer mid-day sunlight added to red light of proven potency, birds invariably passed the climax of testis size and activity, and underwent regression; that this regression was more or less independent of the proportions of ultra-violet or of green in the light used; and that it was probably due to the "throwing out of gear" of some part of the sex mechanism. It was impossible to maintain maximum testis size and activity indefinitely, even on the most stimulating exposures to light used. The data indicated that the time occupied by any phase of the sexual cycle bears an inverse relation to the effectiveness of the light stimulus (11).

A further grant from the Grants-in-Aid Committee of the National Research Council enabled the writer to study at Cambridge, to extend these studies on the starlings, and to try the effects of similar light exposures upon mammals with similar types of sexual periodicity. An unsuccessful attempt was made to determine whether the light entered the birds through the heads, because, on the reduced diet used, and with the handling of the birds twice daily to put on and remove hoods from half the birds in a cage, all the birds in the cage died before the results were evident. However, some birds were kept successfully on a diet restricted to "middlings" mash, low in proteins, fats and vitamines, under treatment with red and green lights, of previously proven potency, for over 22 days. On this diet red light did not induce marked testis activity, as it had done previously on adequate and mixed diets, and green was, as before, inhibitory. This result was taken to indicate that restricted diet may act as a limiting factor in the induction of sexual activity by stimulating exposures to light (Unpublished data). On the adequate diet previously used, similar red light, of somewhat less intensity, induced complete spermatogenesis in 20–23 days (9, 10, 11). These results indicate that, if either the light exposures or the diet be too restricted, sex-gland activity fails to occur. This may throw some light upon the sexual cycles and reactions of birds in the tropics, as these may be related to the seasons and to food and light changes.

As these studies stand, both light and diet appear to be factors in controlling sexual cycles in starlings—light, however, much more than diet. These experiments also indicate that the differences in effects induced by red, green, and white electric lights, with or without ultra-violet, are due to wave-length specificity, and not to the heat intensity to which the birds

are subjected by the exposures to light (9, 10, 11, 12).

EXPERIMENTS ON FERRETS

Ferrets were chosen for work at Cambridge, as the mammal most suitable for an investigation of the relation of light to sexual cycles in mammals, partly because the female sexual cycle of that animal has been so thoroughly studied by Drs. Marshall and Hammond of the Institute of Animal Nutrition of the School of Agriculture there, and partly because the swelling of the vulva of the female signals the coming into oestrus of the animal. No attempt has yet been made to analyse completely, or even very thoroughly, any of the aspects of the problem; but the effort has been made to find out the general possibilities and the amount of plasticity of the ferret as experimental material, in this connection. The experiments have been preliminary only, and the numbers of animals used in the various modifications of the light exposures have been small (35 in all). It was desired to find out if the sexual cycles of both sexes could be modified at will, in the direction both of complete oestrus and spermatogenic activity and of complete cessation of activity or anoestrum. All the experiments reported on, for this animal, are open to the objection that the numbers used were small and the results, therefore, inconclusive from a quantitative standpoint. This limitation of the work must be kept in mind while the report and discussion proceeds.

As pointed out above, the sexual cycle of the female ferret has been thoroughly studied by Dr. F. H. A. Marshall (13) and Dr. John Hammond with Dr. Marshall (14), of the Animal Nutrition Institute at Cambridge. That of the male ferret has been studied by Miss Marjorie Allanson of King's College, London (15). These cycles resemble those of starlings sufficiently to make studies on the ferret comparable to those already made on starlings, and described above. The swelling of the vulva of the female ferret indicates when she comes on heat,—a great convenience in such studies. Effective copulations, as to time and duration, were taken as criteria of activity of males at first. That this was none too good a test has since been discovered.

Experiments were begun on October 12, 1931, by subjecting three male and three female ferrets to electric light, after dark, from a 200 watt bulb, at such a distance as to throw light directly on the ferrets whenever the light was turned on. Luminous intensity ranged from 14.1 foot candles, at the front of the top cage of each row, to 4.88 foot candles at the back of the lowest cages. This light was turned on for 6–6½ hours each night after sundown, by a time switch, and light was freely admitted to the room during the day through a large window facing the cages. Two males and five females were kept as controls in a similar room across the hall, with similar temperature, food, and care, except that the light-treated animals were denied nesting boxes and given too little shavings to permit them to hide from the light. This prevented them from keeping as warm as the controls.

Two of the experimental males died on November 18th and 25th, after 37 and 44 days of exposures to electric light. The cause of death of one was unknown,—possibly distemper. The other died from abscesses in the throat and top of the head. These illnesses were not likely to increase the effects of the light treatments, but rather to retard them. So the testes were taken for study. One of the control males was transferred to the lighted room in place of one of those that died, leaving only one control male. Neither room

was artificially heated and the experimental animals were kept colder than usual, or than the controls, by being deprived of excess shavings.

By November 23rd, (42 days) two of the three females were on heat and the third was found to be hiding from the light by burying in the shavings. She did not come on heat till after the shavings were reduced on December 1st, reaching complete heat by December 20. These three females were mated with the original light treated male on December 10, 11, and 21 respectively. They became pseudo-pregnant and underwent all the changes usual to this condition, such as shrinking of the vulva, enlargement of mammary glands and teats, darkening of the areola round each teat, and shedding of some fur. Since ovulation and pseudo-pregnancy occur, in the ferret, only after prolonged copulation, these changes were taken as evidence of ovulation. Whether the ova shed at these times were normal and capable of fertilization, or not, remains to be tested. No sperms were found in the fluid from the vulvae of these females after these matings. A motile fluid with flagella-like bodies, presumably from the epididymis, and epithelial cells, normal for oestrus, were found.

On the male side, the two males that died had undergone some stimulation of germ-cell multiplication and considerable interstitial cell increase. Epididymides were modified considerably in one and not in the other. Comparison was made with conditions in testes and epididymis from a male bought from a dealer and killed on December 12th, without light treatments. These two males had not been tried with females in oestrus, because previous to their deaths none of the females were yet in oestrus, or the males were too ill to bother with them. The other light treated male showed marked libido; his testes were enlarged, and had moved posteriorly, from the winter position in the groin, to the bottom of the scrotum below the anus, where they protruded, and the hair over the scrotum had begun to thin out. He mated successfully with all three females as above described. On December 22, the day following a copulation lasting one hour and forty minutes, he was sacrificed, and his reproductive organs, pituitary, thyroid, and adrenals were taken and fixed for study. No sperms were found in his epididymis, nor in the seminiferous tubules. The latter were enlarged, as compared with those of the normal ferret killed on December 12th, and more germ-cell generations were found. Interstitial tissue was much increased and the epididymis was like that of a normal breeding ferret except for the lack of sperm contents (16).

The libido of the male transferred from the control to the light room on November 25th was quickly stimulated so that he tried persistently to copulate.

On December 7, 12 and 15, more males and females were added to both control and experimental rooms and their light exposures measured as to time and intensity; since it was evident that ferrets are susceptible of modification of their sexual cycles by changes in amounts of exposure to light, somewhat as the starlings are.

All light treated females of the new additions as well as those three of the first (pseudo-pregnant) group, so treated, came into oestrus and were mated with light stimulated males on February 2, 3, 8, 12, 17, 18, 29, and March 1, except one of the first three, which came into oestrus on March 12 and was not mated. She was kept in oestrus to see how long she would stay so. She remained in oestrus, as is usual with unmated females in summer, till after her daily period of exposure to light was reduced from about 18 hours to

about 16 hours per day, when she went off oestrus and her vulva shrank toward winter condition in May.

Pseudo-pregnancies again resulted in the cases of all these matings, except that on March 1, which led to a litter of 8 young, born on April 11, (unfortunately only 3 days earlier than the earliest litter obtained by Marshall and Hammond in their studies of pregnancies and pseudo-pregnancies in ferrets) (14).

Motile sperms were found in the fluid removed from the vulva or vagina after copulations from February 8th onward; but the numbers were small and their motility low till matings on February 29th. This low concentration and feeble motility would account for the failure of fertilizations and so for pseudo-pregnancies instead of real pregnancies, on those dates. Even in summer, a low concentration of sperm, in the smear from the vulva after copulation, is associated with pseudo-pregnancy only (14).

Some of these females again came into oestrus in April and were transferred to the control room with the daylight period reduced to about 7½ hours per day. They went off heat, even in this, the normal, period of heat in ferrets. Between October 12th and April 1st, no control female showed any sign of coming into oestrus, though all the experimental females had been pseudo-pregnant at least once, and some three times, before April 15.

The original control male, kept on short light schedule, showed little or no interest in females in complete oestrus and made no real attempts to copulate with them. Light-treated males copulated, whether they were fertile or not. They were potent; he remained impotent, on the short days, even up to March 21st when he was sacrificed and sperms were found in his testes, which were in complete spermatogenesis. His epididymides were full of sperm, and his testes large. An experimental male killed at the same time was in somewhat the same condition of testes and epididymides. So were males recently bought, and put on light treatments for 10 days or on short days for 28 days respectively. A study of these testes has not yet been completed except to ascertain that all were at complete spermatogenesis. Whether the light treatments cause males to produce sperms any earlier than is normal has not yet been learned.

To test whether or not the light causing these changes is received through the head and eyes or through the general body surface, four female ferrets from the control room, with previously restricted daily light exposures, and showing no signs of heat or oestrus, were moved to the light room on March 4th. Two of these were hooded each night, from 4 P.M. till 9 A.M., with black velvet hoods covering the whole head and tied behind the ears,—during the time the light was turned on, as well as part of the daylight exposure period. The other two, placed in exactly the same relation to the lighting systems, were not hooded, but received the light over their whole bodies. The previous light history of these two pairs of ferrets had been the same. The two unhooded ferrets came on full heat by April 9th, were subsequently mated and pregnant. Of the hooded animals, one showed no sign of coming on heat at all till she died on May 8th, from tuberculosis; the other showed first signs of vulval swelling on April 14th, but did not reach complete oestrus till May 18th when she was mated with a black ferret and with a white one the following day. Her coming into complete oestrus was slowed up by a reduction of the daily exposure to electric light by one hour on May 5th. These two hooded females were slower in coming into oestrus than females kept in the control room behind curtains for the same periods each night, and receiving no electric light after dark. Some

light filtered round the edge of the curtain and could be picked up by those animals behind the curtain, if they focussed their eyes upon the beams, so passing the curtain. Other modifications of the periods of exposure to light have been tried and the results are consistent with those above described. They will be included in the description of the study in detail, to be reported elsewhere, when finished.

It is enough to say here that increasing intensity of illumination, as spring advanced, during the 7½ hours when the ferrets on restricted exposures were receiving light, caused female ferrets to come into oestrus, while at the same time a reduction, of one to two hours, in the period of added electric light, received by ferrets on a total exposure of about 18 hours per day, resulted in females going out of oestrus without being mated, after they had been brought to the full oestrous condition by such long exposures.

These results lead to the tentative conclusions that increase of either duration or intensity of the daily periods of exposure to light or of both, causes increased sexual activity in female ferrets, leading to complete oestrus, in time; in male ferrets, it induces some increase in germ-cell activity and great increase of interstitial cell mass and, probably, of activity, with increase of libido and the production of a condition of the epididymis similar to that of the normal breeding ferret. Reduction of either period or intensity of the exposure to light leads to an anoestrous condition, in females, and to loss of libido and of testis size, in males. The exact reactions of males to these changes require much further study.

IS THE HYPOPHYSIS INVOLVED IN THE REACTION?

Results obtained by others, after treating male and female mammals with anterior lobe pituitary substances, and particularly those of Hill and Parkes (17), in London, with ferrets, lead to the strong suspicion that the anterior lobe of the hypophysis is involved in these reactions. But further study is needed before one can offer any very complete or definite theory as to the mode of its action. It appears probable that the light rays, of the long-waved sort, react upon some part of the head of the ferret and, through that receptor, upon the anterior lobe, to stimulate it to increased secretion or liberation into the blood stream of the hormone which causes increased gonadal activity, and that this increase leads to activity of the secondary sex mechanism involving the uterus, vagina, vulva, and behaviour, in females, and the epididymis, penis, and behaviour, in males. Whether this receptor is confined to the eyes or to the naked skin of the face and ears has not yet been ascertained. Ferrets with cataract or opaque lenses react in the same manner as those with normal eyes. So that, while one may suspect the eyes as the receptors, a clear image is not necessary to the effect. More than that, sleeping, and very inactive ferrets react just as well as active, wakeful ones. This suggests that whatever part of the spectrum is effective in ferrets must penetrate at least the skin of the eyelids before reaching the receptor proper, which mediates the action to the sex mechanism. A neuro-humeral effect, of the sort described by Parker (18), is suggested.

Different parts of the spectrum have not yet been tried with ferrets; but the necessity for ultra-violet is excluded by the fact that all these ferrets were behind ordinary window glass throughout the experiments. From the results with starlings, one is led to suspect the long-waved red light as effective with ferrets also. But it is quite possible that some region other than that effective in starlings may be the one most potent in modifying the sexual cycle of the ferret.

Studies on the relations of daily period of exposure to light to sexual activity and to seasonal sexual cycles in a mammal have been made by Baker and Ranson (19), of Oxford, England, using voles as experimental material. These studies lend support to our findings with ferrets, that the female sexual cycle is conditioned to a great extent by seasonal variations in daily exposure to light, while that of the male is less so. They also used electric light under controlled conditions. They have found, in addition, that type of food plays a considerable part in the reaction. In that they agree with our findings for starlings.

All the studies referred to above indicate that seasonal sexual cycles in, at least, some birds and mammals, are conditioned to a very considerable extent by seasonal changes in the duration and intensity of the daily periods of exposure to light of the visible or long-waved sort, and that, in birds at least, red light is more effective in this respect than shorter waved light. In birds, both sexes appear to be equally dependent on variations in exposure to light for their seasonal changes of sex-gland activity. In the mammals investigated, females are much more completely controlled in this way than males, under the conditions of experiment so far used. It is increasingly apparent that diet also affects the reactions of birds, at least, to the light induced changes and that it may even act as a limiting factor in this respect. This may very probably be because of deficiency in vitamines and proteins already known to be essential for normal reproductive rhythm, and capacity.

The whole problem requires, and would seem to be likely to repay well, much further study under well controlled conditions. The fact that the anterior lobe of the pituitary seems to be involved in the reaction as a mediator of the effect upon the sexual apparatus indicates the need for coöperation of those engaged in the study of sexual photoperiodism with the numerous students already so far advanced in the study of the intimate correlation of the activities of the anterior lobe of the hypophysis, the gonads and other sex apparatus, and of the thyroid and adrenals as also likely to be involved. This has been discussed elsewhere in more detail (11, 12, 16).

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* The Quarterly Review of Biology, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

WARNING COLORS AND MIMICRY

Being a review of *The Zoological Society's Expedition to the Zambesi, 1927. No. 4. On the Ecology of Tree-frogs in the Lower Zambesi Valley, with special reference to Predatory Habits considered in relation to the Theory of Warning Colours and Mimicry,* By Hugh B. Cott. *Proc. Zool. Soc. London,* 1932, Part II (July), pp. 471–541, Pls. 1–2.

By W. L. McAtee, Cherrydale, Va.

One certainly must have the true religion to uphold selectionist doctrine relative to the so-called protective adaptations of animals. If we may judge from current practice, he must accept the most tenuous whimsicalities of his forbears as if they were respectable theory and he must so far abdicate his intellectual integrity as to make assertions that do not agree with his own data, much less with the observed facts of nature. In other words to be a good selectionist, he must stultify himself at every turn.

The latest example is furnished by Hugh B. Cott, a disciple of that arch-selectionist Professor E. B. Poulton of Oxford University whom he profusely thanks.

In publishing on the tree-frogs of the Lower Zambesi Valley, this author mixes with the warp of fact derived from collected specimens the woof of stereotyped selectionist phrasings, which to change the metaphor but not the word is simply woof, woof!

Speaking of a boldly brown and white striped tree-frog (*Megalixalus fornasinii*), he says (p. 475) "To human eyes at any rate, the creature ceases to bear any marked resemblance to a frog," while at the same time he publishes illustrations that show quite clearly it does look like a frog. He goes on to say that posture (which by the way is just like that of other tree-frogs the world over), and pigment combine to distract the observer's attention and effectively to mask the identity of the frog, while a few pages previously he informs us that he collected within 24 hours of his arrival 802 frogs of which 381 were of this species, and 289 of three other kinds together.

He is convinced that the creature benefits in being enabled to capture more alert prey "because its attitude and 'ruptive' colour scheme combine to take away its frog-like appearance." (p. 476). What matter to its victims whether it is frog-like or unfrog-like? It is one of the things that gets them and if they react defensively at all, it would be in relation to what the frog is—an enemy—without regard to kind.

Of its prey, he mentions dragon-flies, grasshoppers, muscid flies, and Lepidoptera as alert and most difficult to capture and says they were "eaten in conspicuously greater numbers" by *Megalixalus* than by the other frogs. The dragon-flies according to his tabulations were damsel-flies, the weakest of their group, most of which can be picked up with the fingers as they hang, wings together, from the tips of grass blades or other perches, and which on the wing are feeble flutterers. The grasshoppers while good jumpers must by no means be difficult to capture as practically all insectivorous predators feed upon them. The statement that they are eaten

in conspicuously greater numbers by this frog than by any of the other species examined is untrue, as 7 Acrididae were found in 360 stomachs of *Megalixalus*, or 1 to each 51.4 stomachs, while 3 were found in 122 stomachs of another frog (*Hyperolius argus*), or 1 to each 40.6 stomachs. Mosquitos are included by Cott in his table of prey difficult to capture, but it is very unlikely that these small fragile insects offer the least difficulty to tree-frog predation. Probably all that is necessary is that they come within reach. The Lepidoptera found in the stomachs of this frog were more than half larvae or caterpillars, mere "worms" to which the terms "active, alert, rapid in flight" most assuredly do not apply. What difference does it make anyway as to whether prey is alert, quick on the take-off, etc., if the mode of feeding, as it is in most frogs, is a lightning-like flick of the tongue that gives no time for alertness to function? The whole argument relative to advantage of this frog in relation to prey is special pleading with little regard to facts but just what would be expected from a faithful disciple of Selectionism.

Cott, while dilating on the powers of *Megalixalus* in capturing prey "active, alert, rapid in flight," says nothing about the much greater prevalence in the food of this frog of the feeble and partly wingless plant lice. He has nothing to say also as to why this frog fed to a considerably smaller extent upon ants (very "specially protected" insects) than did any of the other species. The average scientist viewing these things in a normal way would assume that because of special habitat, size, or other factors *Megalixalus* simply finds it convenient to subsist upon a somewhat different assortment of prey from that taken by the other frogs. That is about all there is to it, and in this effusion, as in many others perpetrated by selectionists, much good white paper has been needlessly dirtied by extended fantastic speculations about happenings, which if viewed in a more moderate and logical way would call for no special comment.

Warning colors are given a flourish in this Zambesi paper and are said to be associated with defensive skin secretions. The frog (*Hyperolius argus*) about which this point is made has the sexes of very different color patterns, the female being allegedly conspicuous although the picture presented would lead one to think it a fine selectionist example of concealing coloration. The male with presumably the same skin secretions is plain. These inconspicuous males, however, are found in the same situations as those favored by *Megalixalus fornasinii*, the most conspicuously colored frog of the entire collection.

To sum up these arguments, the most strikingly colored (broadly brown and white striped) frog the author treats is held to illustrate the "disruptive" type of concealing coloration, while one which is brownish with "eye-spots" almost matching some of the holes on a leaf on which it sits, is said to have "a colour pattern that is at once striking and distinctive" (p. 477), i.e., warning, and the author ventures to predict that these "frogs will be found to possess some defensive secretion which renders them undesirable as food" (p. 478).

The plates illustrate four species of frogs, one plain green, one brownish with orange ocelli, one finely striped yellow and black, and one broadly striped brown and white. All are said to be protected in one way or another. The appetite of the selectionist for "protectedness" is as insatiable as it is indiscriminating. Plainly, the motto is "Whatever is, is right," and the attitude of mind differs in no essential from that of the special creationist, whose position Darwin was so at pains to challenge. Were Darwin alive now, he would have the mortification of seeing what are said to be his ideas held as dogmas, and accepted with an unwavering faith and promulgated with a fanatical zeal which have no part in science.

The truth is that acrid or poisonous skin secretions are of common, perhaps of universal, occurrence among frogs and toads. Some of these animals are plainly, others conspicuously, colored, but what of it? The group exhibits a great variety of color patterns and almost every imaginable intergradation thereof. But must each be held significant, a definite meaning asserted, and a highly theoretical explanation of it be made in every case? Em-

phatically no; adaptations that apparently will serve in one case, in another will not; in endeavoring to explain them all, the whole effort becomes a hodge-podge of error, misconception, and misstatement that only the stoutest can stomach.

Cott says on a single page (and even these fallacies are not all that can be gleaned there):

> The adaptive significance of colour in frogs has been little studied in the past, and I am persuaded that research will prove that colour and pattern play a much more important part in frog-ecology than is generally imagined. . . .Poisonous skin secretions are of common occurrence among the Anura. In many species they are known to furnish an effective means of defence against predatory enemies. . . . Snakes and birds, the principal enemies of frogs, depend largely upon vision in hunting for prey. There is evidence that these enemies learn to discriminate between poisonous forms and those which are good to eat. (p. 478).

These extracts make a very good one-page record of assumption, misstatement, and error even for a selectionist. He is persuaded that colors are important in frog-ecology, but self-persuasion in the lack of evidence is something entirely out of place in science. "In many species," he says, "poisonous skin secretions are known to furnish an effective means of defence." If the word *many* is taken at its ordinary valuation, this is a definitely untrue statement. Take the next remark, that snakes and birds learn to discriminate between poisonous forms (of frogs, by implication) and those which are good to eat. There is no evidence of any frog being dangerously poisonous either to snake or bird predators upon it, hence the discrimination alleged is a myth.

The author notes that snakes are very abundant in the region of the study, and goes on to say: "Tree-snakes are undoubtedly their [i.e. the frogs'] greatest enemies. Tree-frogs are never beyond the reach of these silently gliding forms. . . . From such there is no safety" (p. 483). This controverts what he has previously said about concealing coloration of the frogs, and paradoxically is further an example of the horrific statements made by selectionists to show the severity of the struggle for existence. The other side of the picture, conveniently forgotten here, is given on p. 474, where it is said of tree-frogs: "Such is their abundance, that in suitable localities . . . a systematic hunt will yield a frog every yard or two. If we calculate the population of such an area in terms of one tree-frog per 4 square yards, or say, 1000 per acre, it is probable that this would not be an over-statement." To the non-selectionist it would appear that where there is a population of 1000 per acre, tree-frogs cannot be experiencing a very severe struggle for existence.

One of the loveliest things about being a selectionist is that the traditions of the school permit argument with entire disregard of the facts. For example, hear Cott on protected insects. After mentioning some lizards that feed upon ants, he says: "But although the adaptations fall far short of perfection, and in some cases prove ineffectual in defence, facts such as these in no way disprove their general usefulness."

It seems futile to present statements of fact to writers of this type. Bequaert (*Bul. Amer. Mus. Nat. Hist.*, Vol. 45, pp. 271–331, 1922) has catalogued and discussed the predatory enemies of ants from spiders to man and says: "There is certainly little or no evidence to show that, as the theory is often expressed, ants are unpalatable to most insectivorous animals and are merely eaten accidentally or 'during the time in which young birds or other animals are learning what to eat with impunity and what to reject.' "

McAtee furthermore summarizes (*Smiths. Misc. Coll.*, Vol. 85, No. 7, 1932, p. 96) information about ant enemies, concluding: "In fact it would be difficult to name a group of insects that is so thoroughly preyed upon as the ants, and impossible to name one that has so many specialized foes scattered through the various animal phyla."

Despite Cott's assertion, the fact is that there is no "general usefulness" of adaptations of ants in relation to predators. The latter take all the ants they want, and the ant supply remaining plentiful proves nothing beyond the fact that there are too many to be eaten up, or for that matter even reduced in numbers.

Cott quotes experimental results tending to show that protected insects are eaten only up to a certain point and not beyond it. This merely indicates satiety, not pro-

tection. A man can eat beefsteak until it palls upon him, but still have an appetite for pastry, and perhaps even for ice cream and candy after that. The reverse, however, is just as true, for, granted a fresh start, after being cloyed with candy, he can again relish beefsteak. Just because a man or a bird does not keep on eating the same item of food indefinitely does not justify the assumption that the food is distasteful (or protected). The whole of the experimental evidence as to edibility of prey is scarcely worth the paper it is printed upon, a fact pointed out by McAtee twenty years ago (*Proc. Acad. Nat. Sci. Phila.*, June 1912). Animals do not react naturally in captivity, they eat things never encountered in life, and they refuse things customarily eaten by their wild brethren. Drawing conclusions as to their natural tastes from abnormal behavior in captivity is entirely unjustifiable. The citing of any amount of experimental evidence as to choice of food leaves the student of the natural feeding habits of animals entirely unmoved.

Cott goes on to say: "An animal is compelled by hunger to eat unpalatable food. If the preferred article is not present, the next best must be taken" (p. 494). This is an absolute misconception of the process of food finding. Animals take what is most available at the particular time and place. Availability of course is qualified by the size of the animal in relation to possible prey, specializations as to food, etc., but in general availability means abundance, and feeding proceeds from the more to the less available items, not from imaginarily preferred or palatable, to the less preferred or unpalatable things. No one who has studied the food habits of wild animals can doubt that availability is in general the controlling factor in choice of food.

A further Cottism (Poultonism by inheritance of course) follows: "It is now fairly well established that an animal's knowledge of what insects are good to eat and what are not has to be acquired in the light of individual experience." There is practically no such distinction as insects good, and not good to eat, for the evidence indicates that all are eaten more or less in proportion to their numbers.

Cott presents a graph (p. 532) and a Table XIV on which it was based showing the food preferences of four species of tree-frogs, of which he says, "I think it can hardly be doubted that the figures in Table XIV point to the conclusion that frogs are not such indiscriminate feeders as is often supposed, that they learn from experience what food is palatable and what is to be avoided, and that they exercise some choice in the manner of diet.' It is difficult to explain the facts in any other way."

Considering the way the curves in the graph for three species of frogs are almost superimposed, and that the fourth diverges notably with respect to only two food items, it is clear that we are reading a record of availability, and that the frogs were feeding more or less indiscriminately on what was available to them.

Cott himself concedes as much in a statement on p. 526 where after commenting on the relatively enormous feeding capacity of the tree-frogs he says: "although these creatures do hunt actively in search of food, especially in the evening, yet they are far less active and mobile than many of the insects upon which they feed, and they therefore must rely upon, and make use of, whatever suitable prey happens to come within their reach—the stomach functioning as a kind of reservoir, ever ready to receive food that chance incidents may render available."

Despite all the evidence as to practical indiscriminacy among prey available to them, the author concludes that tree-frogs are selective agents in the production of warning colors and mimicry and says that analysis of stomach contents lends indirect support to this conclusion. Let us consider briefly the single item of ants; of 11,428 insects identified from about 800 frog stomachs, 9937 or 87 per cent consisted of ants. These insects were not only highly available, therefore, but they were eaten with the greatest freedom. Cott himself has to conclude that "there is little evidence that the defences of ants are in the least degree effective against the predatory attacks of batrachians," a conclusion which is equally true of numerous other groups of predators.

Ants, nevertheless, have always been

hailed by selectionists as aggressive, well armed, highly "protected" insects, and ant mimics have been recorded by the score. If there can be numerous ant mimics in the absence of a scintilla of evidence that ants are protected from predators, the theory of their origin by natural selection collapses, and the theory failing in such a case, it fails in all. Selectionists may ignore facts presented by their opponents but how they can forever ignore and misinterpret those presented in their own writings, can only be explained on the ground that their belief in natural selection has become a sort of religion. In fact we seem to have in selectionists the kind of people who before the day of Darwin would have been special creationists. They are just the same sheep even if in another fold.

BRIEF NOTICES

EVOLUTION

Studies on the Variation, Distribution, and Evolution of the Genus Partula. *The Species Inhabiting Moorea. Carnegie Institution of Washington Publication No. 410.*
By Henry E. Crampton. Carnegie Institution of Washington, D. C. \$13 (paper); \$14 (cloth). 9 x 11½; vi + 335 + 24 plates; 1932.

This is the third volume of Crampton's studies of the land snail *Partula*, the first having been devoted to the species of the neighboring island of Tahiti and the second to those of the Mariana Islands. The author's first exploration of Moorea was in 1907 and 1909, while in 1923 and 1924 the island was again explored in greater detail. In this short time changes in the varieties had occurred.

> In some instances varietal differentiation has gone forward with truly remarkable rapidity, and this process seems to be continuing to a noticeable extent. It would not be expected that the novel differences would amount in degree to distinctions of *specific* value, but they are the same in nature as such distinctions, and are to be regarded as actual steps in the direction of specific evolution.

The factors underlying this differentiation are, the author concludes, genetic in character. In some cases the evidence of mutation is unassailable, embryonic offspring being found in the brood-pouch of a parent from which they differ in the mode of coil. In no case is there evidence that environmental conditions are causes of organic differentiation. Certain species occur only in sharply restricted territories not marked off by any environmental peculiarities, while

> *Partula tæniata* exists in association with all of these forms as one and the same species. Obviously it would be inconsistent to attribute the like qualities of the members of *Partula tæniata* to supposedly similar circumstances throughout the island and at the same time to refer the distinctions of the other species to diverse external conditions.

The distribution of the species of *Partula* in the various Pacific islands is only explicable, the author concludes, on the hypothesis that the islands are the remnants of a vanished continent. The alternative theory of human transport of the snails from one island to another may account for some cases but not for most.

The book is illustrated with beautiful color plates of the shells and with photographs of the environment. There is, unfortunately, no index.

Huxley Memorial Lectures 1925–1932.
By E. B. Poulton, Sir Peter C. Mitchell, G. Elliot Smith, F. O. Bower, Graham Wallas, Sir Arthur S. Woodward, Aldous Huxley. Macmillan and Co., London. 2s. 6d. net. 5¼ x 8¼; 172 (paper).

In 1925 the Old Students' Association of the Royal College of Science, with which Huxley had so long been associated, commemorated the centenary of his birth through a memorial lecture. The success of this determined the Governing Body of the Imperial College of Science and Technology to establish an annual lecture, of which the fruits of the first seven years are here gathered together. E. B. Poulton's biographical lecture on Huxley heads the list; Sir Peter Chalmers Mitchell points out the dangers of stretching a generalization from the known to the unknown;

G. Elliot Smith's lecture on "Conversion in Science" is largely given over to an exposition of his own diffusionist views on human culture; F. O. Bower considers "The Origin of a Land Flora;" Graham Wallas deals with the relation between physical and social science and the academic organization of student-research; Sir Arthur Smith Woodward with "Modern Progress in Vertebrate Palæontology;" while Aldous Huxley analyzes his grandfather's achievements as a literary artist.

THE GEOLOGICAL HISTORY AND EVOLUTION OF THE HORSE. *Geology, Leaflet 13.*

By Elmer S. Riggs. Field Museum of Natural History, Chicago. 40 cents. 5½ x 8½; 54; 1932 (paper).

This leaflet tells the familiar story of the evolution of the horse, based upon a comparison of the fossil remains of successive geological periods. The bony structure of the modern horse is first considered, as a basis for comparison. The history of the horse through the different geological periods is then outlined, after which modifications in the skeleton are traced in detail. Among the more important changes which are evident are: (1) an increase in size, the earliest horse, *Eohippus*, being no larger than a fox; (2) a change in the proportions of the head, especially evident in the jaws and teeth; (3) a change from a broad-footed, four-toed animal which walked on a pad beneath the toes, to an animal walking on a single toe with a broad hoof; (4) a change in habit from a lowland or woodland animal to a strong, swift inhabitant of the plains. There are nineteen plates, and a bibliography of fifteen titles. An excellent popular treatise, which should be particularly useful to high school and college teachers of biology.

THE MECHANISM OF CREATIVE EVOLUTION.

By C. C. Hurst. The Macmillan Co., New York. $6.00. 7¼ x 9¾; xxi + 365; 1932.

So numerous have been the discoveries of biology in recent years that the writer has gathered together the "multitudinous facts which go to make up the genetical story of creative evolution, lest essential synthetic values may be lost in a maze of detail." The rediscovery of Mendel's law and the rapid growth of this line of work has brought about a revolution in biology. An exact science, according to Hurst, has developed out of the discoveries concerning chromosomes and genes and their interrelations. He has brought all of these findings together in an impressive array. The book is abundantly illustrated with excellent figures and diagrams, has a lengthy literature list, and a detailed index.

URSPRUNG DER MENSCHHEIT. *Über den engeren Anschluss des Menschengeschlechts an die Menschenaffen.*

By Hans Weinert. Ferdinand Enke, Stuttgart. 21 marks (paper); 23 marks (cloth). 6½ x 10; xii + 380; 1932.

Beginning with Haeckel's *Anthropogenie* (first published in 1874) the author reviews critically the literature through 1931 concerning the evolution and origin of man. He arrives at the conclusions that the chimpanzee and *Homo sapiens* originated from the same anthropoid stock, which split off in the late Pliocene or early Diluvian period, and that the limits of man's Eden cannot be definitely defined. It probably includes Eurasia, possibly Africa. The book has a bibliography of 14 pages, and subject and author indices.

GENETICS

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture I. On the Genetic Significance of Hemilateral Asymmetry in the Vertebrate Organism.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 38; 1932 (paper).

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture II. On the Making of Use Acquirements; the Neuro-Psychic and Other Responses.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 44; 1932 (paper).

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture III. Genetics in Relation to Public Health and Preventive Medicine.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 34; 1932 (paper).

ON CERTAIN ASPECTS OF HUMAN BIOLOGY. *The University of Birmingham, Faculty of Medicine, William Withering Lectures, 1932. Lecture IV. On the Influence of Environmental Conditions on the Shape and Constitution of the Red Blood-Cell. Lecture V. On the Clinical and Biological Significance of the Above Observations.*

By C. J. Bond. H. K. Lewis and Co., London. 2s. 6d. net. 5½ x 8½; 57; 1932 (paper).

A series of lectures planned for a rather general audience and covering a wide range of subjects. In the first lecture the author discusses the inheritance of asymmetry in animals and in man. Lecture II discusses the way changes occur in the cell structure and function which constitute what the author calls "Use-Acquirements." Lecture III gives a brief summary of human genetics and a program of eugenic reform. Lectures IV and V describe the results of research upon certain aspects of the physiology of the red blood cell.

VARIATION ET MUTATION EN BACTÉRIOLOGIE.

By J. G. Marchal. Librairie Le François, Paris. 50 francs. 6½ x 10; vii + 307; 1932 (paper).

The first fifth of this book is devoted to an historical account of researches on variability in bacteria, protozoa, and metazoa. In the remaining portion the author describes his own experiments on the production of temporary variation and mutation in single cells of bacteria by the use of various chemicals in culture media. He used *B. coli mutabile* Neisser, *B. caryocyaneus* Beijerinck-Dupaix, *B. pyocyaneus* Gessard, and *B. prodigiosus* Ehrenberg. He conducted these experiments with the hope that his results would throw more light on genetic mechanisms in higher organisms, but concludes that more work will have to be done to separate phenotypic and genotypic changes, before microbiology can contribute effectually to the general study of genetics. There is a bibliography of 18 pages.

INDIVIDUALITY OF THE BLOOD *in Biology and in Clinical and Forensic Medicine.*

By Leone Lattes. Translated by L. W. Howard Bertie. Oxford University Press, New York. $7.50. 5½ x 8⅝; xiv + 413; 1932.

This is a translation of a book which was first published in Italian in 1923. Later German and French editions were issued. In each edition the work has been revised and enlarged to keep abreast of the rapid advance made in the field. New matter has been coördinated with old and obsolete material eliminated. The main sections deal with (1) individual reactions of normal blood, (2) hereditability, (3) individuality of the blood as an ethno-anthropological fact, (4) individuality of the blood in its clinical applications, (5) individuality of the blood in forensic medicine, and (6) technique of the individuality reactions. The work includes numerous figures and tables, a bibliography of 2,375 titles, and author and subject indexes.

GENERAL BIOLOGY

ANTONY VAN LEEUWENHOEK AND HIS "LITTLE ANIMALS." *Being Some Account of the Father of Protozoology and Bacteriology and His Multifarious Discoveries in These Disciplines. Collected, Translated, and Edited, from His Printed Works, Unpublished Manuscripts, and Contemporary Records.*

By Clifford Dobell. Harcourt, Brace and Co., New York. $7.50. 7¼ x 9¾; vii + 435; 1932.

All things happen for, as well as to, him who waits. We have been wanting for a long time an adequate account of the life and labors of Antony van Leeuwenhoek. Paul deKruif's chapter in *Microbe Hunters* about him was good, but only as an appetizer. What was needed was a good, solid, substantial meal. Now we have it. One of the greatest figures in the whole history of biology receives at last his just due—a worthy biography. And it *is* worthy,

even of so great a man. At the moment the only biography of a scientific man that we can think of as at all to be considered in the class with this great work is Pearson's *Francis Galton*. Dobell's knowledge of protozoa and of biological history, and of their cognate subjects, is simply colossal, both in depth and range. Furthermore the painstaking and enormously laborious care he has taken to verify from the original source every minutest detail touched upon in the book and capable of being verified, is almost without parallel in modern historical work in the field of science. So also is Dobell's modesty about what he has done. One stands humble and abashed before such a monumental example of scientific scholarship.

Antony van Leeuwenhoek was a difficult subject for a biographer. He knew no language but his own, now archaic, brand of Dutch. Furthermore he was neither a "professor" nor a "doctor" but just an honest shopkeeper (dry goods and notions) who had an interest in looking for, and seeing things for himself, and then telling other people who might be interested about what he had seen. He did the telling chiefly by writing long letters to the then newly founded Royal Society of London. These letters were then translated, and edited, and in some part published. The result of this roundabout technique was to leave considerably less than a perfect record of what Leeuwenhoek really said and meant, but, as Dobell shows, few persons since have taken the trouble to study seriously even these inadequate records.

The author had two primary objects in the preparation of this volume: The first to give an adequate English translation of such part of Leeuwenhoek's original writings as bear upon protozoa and bacteria (and incidentally on some other biological matters); the second to give as true and complete an account as possible of the manner of man he was and how he lived his good and useful life. These objects, together with voluminous, detailed, erudite, witty, and humorous comment and annotation along the way, have been superbly accomplished. The volume is beautifully produced. There are 32 photogravure plates besides text figures, and an excellent detailed index.

This is a very great book. No biologist can call himself educated who has not both read and studied it.

HUMAN BIOLOGY

PROBLEMS OF POPULATION. *Being the Report of the Proceedings of the Second General Assembly of the International Union for the Scientific Investigation of Population Problems. Held at the Royal Society of Arts, London, June 15–18, 1931. Published under the direction of the Executive Committee.*

Edited by G. H. L. F. Pitt-Rivers. George Allen and Unwin, London. 15 shillings net. 6 x 9¼; 378; 1932.

This volume of Proceedings contains the full text of all scientific papers presented at the London meeting of the International Union for the Scientific Investigation of Population Problems. The business proceedings, which have already been published in the *Bulletin* of the Union, are not repeated here. The authors of the papers address themselves to many different aspects of the population problem and sometimes obtain different answers to the same question. Thus while Fischer for Germany and Notestein for the United States concur with earlier investigators in finding an inverse relation between social status and fertility, Edin finds that in Swedish cities the relation is changing from inverse to direct. A number of the papers are devoted to the forecasting of population trends. Thus Reed, on the basis of his saturation curve, concludes that, while the proportion of gainfully employed women in the United States is increasing, it will not become as large as that of gainfully employed men, but that "we are tending toward a position where we shall have one gainfully employed female for every three gainfully employed males;" Whelpton, on the basis of projected trends in specific birth and death rates and in net immigration, concludes that the population of the United States will reach a maximum of 144,600,000 in 1970 and will thereafter decline; Dublin views with alarm the decline in the American birth rate; and Baudhuin forecasts a maximum in the Belgian population as early as 1940

and a marked fall after that. Lotka works out mathematically and by means of numerical examples the changes in the birth rate, death rate and age distribution of a population growing according to the logistic law. Hankins concludes that the fall in the birth rate of western peoples is probably due, not to racial senescence, as Gini contends, but in part to birth control and in part to the physiological effect of the rising tempo of social life. Fawcett considers the effect of natural resources and social organization on population density. Gregory points out that "the ultimate effects of the suppression of migration are . . . likely to be more unfavourable to the immigrant than to the emigrant country." Elton deals with the migrations of animal populations. Crew describes his experiments on populations of mice, which show that while the death rate, reproductive rate and fecundity of the population are affected by population density, there are many individuals which endure with ease the conditions of density to which they are exposed. Altogether these papers represent a notable contribution to a subject of great importance to the world. The value of the book is enhanced by an index.

THE ESKIMOS. *Their Environment and Folkways.*

By Edward M. Weyer, Jr. Yale University Press, New Haven. \$5.00. 6 x $9\frac{1}{4}$; xvii + 491; 1932.

The first half of this outstanding treatise on the Eskimo was presented as a doctoral thesis at Yale. The author, a member of the Stoll-McCracken Arctic Expedition in 1928, does not deal with his experiences as an explorer in the far north (not once does the personal pronoun *I* appear) but has compiled a study of the primitive Eskimo as he exists in his natural conditions, and the adjustments he had made to his original environment before outside influences intervened. Many previous explorers have paved the way for this work. The result is a summing up of all available knowledge concerning the specialization of a race which has had to cope with the most difficult of all environments. More widely distributed than any other primitive people (from East Cape, Siberia, to Eastern Greenland and Labrador), the Eskimos number at present roughly 36,000 individuals. In spite of being thinly scattered over so vast an area they exhibit a culture that is "at once broadly uniform in all its subdivisions and distinct in a large measure from every other culture of the world." Second only to "the marvel of their perfect adjustment to their environment is their conformity to the broadly human traits of mankind." The Eskimos' confidence in tradition is tremendous, and they are deeply influenced by their religion, which is closely connected with the affairs of every day life, such as hunting, cooking, eating, and curing disease. Their finest artistic achievement is in the making of masks. This proficiency doubtless developed out of the custom of destroying the masks at the termination of each ceremony.

The author draws heavily on the notes of such dependable observers as Jenness, Birket-Smith, Stefansson, and many others. In each case the reader is referred to the original source. The excellent maps and the table showing the taboos pertaining to game animals increase the usefulness of the book. The work includes a lengthy bibliography and an excellent index.

MAN'S ROUGH ROAD. *Backgrounds and Bearings from Mankind's Experience.*

By A. G. Keller. Frederick A. Stokes Co., New York. \$3.00. 6 x $9\frac{1}{4}$; viii + 450; 1932.

This book is based on the four volume *Science of Society* by Sumner and Keller. It needs no recommendation to the informed reader. To those who have not the time or the opportunity to read the larger work this volume will be most welcome. The main divisions are: Adjustment, maintenance, religion, propagation and gratification. Each of these consists of several chapters. For example, under religion the chapter headings are: The luck element; The spirit-environment; Fetishism; The ghost-cult; Daimonology; Worship and sacrifice; Magic and science; The medicine-man; and Religion in general. Under prop-

agation: Marriage; Preliminaries to wedlock; Wedlock and the status of woman; The dissolution of wedlock, plural and pair-marriage; Posterity and the family. A searching analysis is made of the primitive period, this being, in the author's opinion, the only way to obtain a sound basis upon which to build a science of society. His reasons are that the primitive period covers by far the longest stretch of society; institutions are here in their lowest terms and in process of growth. Furthermore, a more complete picture of the *whole* of social life can be obtained than by a study of history, which yields facts chiefly relating to politics and the "great man."

The book does not present a panacea for our present ills, but

> a point of view from which to scan the institutions by which we live. It stands for the necessity of knowing the anatomy and physiology of society before hanging out a shingle. It promises no immediate results, even from such study. It opposes no programs that represent the best we can do with the knowledge we have. But it calls for the patient effort to develop a pure social science, even if that seems to be a forlorn hope, as a necessary prerequisite to an applied social science.

Since the book is primarily for the general reader rather than the student, neither reference lists nor index are given, but the arrangement of material very closely follows *Science of Society*, where will be found a large bibliography and an index which is highly useful.

AT HOME WITH THE SAVAGE.

By J. H. Driberg. William Morrow and Co., New York. \$3.50. $5\frac{1}{4}$ x $8\frac{1}{8}$; x + 267; 1932.

This is a book which all who expect to come in contact with the so-called uncivilized races should read. While the author, who was in service for fifteen years in Uganda and the Sudan, writes more particularly of the African native, what he has to say in general concerning the importance of the understanding of tribal mores will be highly useful to anyone visiting a community of primitive people. The early chapters deal with the general aspects of social anthropology; the latter part with manners, magic and religion, economic life, law, education, etc. The main emphasis throughout the book is on the rigorous training from childhood which the individual receives in all forms of polite intercourse and tribal customs. He is in no sense carefree, but must conform to definite and often elaborate codes of behavior. While 800 words will suffice the average English speaking individual, the savage must frequently master 2,000. The young must be deferential towards their elders. At a communal hunt if a young boy first perceive the lion he must quietly say that a hyena (a harmless animal) is in the vicinity, in order that he may not unduly alarm anyone. On the other hand, should a stranger speak to a child he must first pick up a handful of ashes and rub it on the child's head. To spit in one group is the most formal of salutations. Sex with all its implications is subject to the most precise regulations and tabus. Primitive law, which demands absolute conformity from all members of the community, has a potent weapon in ridicule, public and formalized.

Professor Driberg's plea is for a more human understanding of the savage. The foreigner who ignores the iron-clad institutions of these people will make little progress in his relations with them. Written for the lay reader the book is not without considerable value to the student. Included in the text are 16 plates. There is a brief bibliography, subject index and an index to tribes.

THE PIONEER FRINGE. *Special Publication No. 13.*

By Isaiah Bowman. American Geographical Society, New York. \$4.00. $6\frac{3}{4}$ x 10; ix + 361; 1932.

PIONEER SETTLEMENT. *Coöperative Studies by Twenty-Six Authors. Special Publication No. 14.*

American Geographical Society, New York. \$5.00. $6\frac{3}{4}$ x 10; vi + 473; 1932.

In *The Pioneer Fringe*, which serves as an introduction to *Pioneer Settlement*, the author gives a general survey of the problems of land settlement. The fact that

pioneering today is a different problem from what it used to be is clearly demonstrated. It involves more than mere acquisition of land; it is necessary to have machinery and tools with which to produce and sell. The pioneer of today aims also at maintaining a higher standard of living than the old pioneer. Part I of this book deals mainly with the general principles, motives, and methods of present day pioneering and the effects of railroads upon it. Part II discusses the regions in which settlers are at present attempting to gain a footing.

In *Pioneer Settlement*, the reader gets a vivid picture of actual present day pioneering, from twenty-six authors, each a specialist and intimately acquainted with some phase of the problems of the region discussed. The book is exciting to anyone in the least interested in population, sociological, and pioneer problems. One sees what the situation actually is in the regions of Western Canada, South America, Manchuria, Africa, New Zealand, and other areas where settlement is taking place. Discussion settles mainly around the agricultural situation. Almost all of the lands now available for pioneering present great difficulties because of their relative infertility.

THE FRENCH RACE: *Theories of Its Origins and Their Social and Political Implications. Prior to the Revolution.*

By Jacques Barzun. Columbia University Press, New York. $4.25. 6 x 8¾; 275; 1932.

An investigation of the writings of the most significant authors who touched upon race conflict and its socio-political ramifications in France before the eighteenth century. The author shows that race origin was far more than an academic question from the sixteenth century to the revolution. The Nordic-Latin-Celtic race theories were back of all the complex problems of government, religion, taxation and social custom. "Class war in all its aspects, interopposition of kings, nobility, clergy and Third Estate employs the ammunitions of race-pride to vindicate its aims and destroy its opponents." The early French nobility held to the theory of a Germanic conquest in the past over the aborigines of the country and to the inheritance of their political rights by the establishment of fiefs by the companions of Charlemagne. The clash between the nobility and the clergy had its origin in this belief. Writings on the subject prior to the fourteenth century are meager and vague but the controversy between the defenders of the Gallo-Roman and the Nordic theories increased as the clash between the nobility and the lower classes developed into warfare. One of the most vigorous of the writers on this subject was Montesquieu. He held to the theory that the Germans were the "fathers" of the French and of their government. On the other hand, Voltaire, while admitting a double conquest of Gaul by the Romans and by the Franks, did not believe in any subsequent racial division or that the Franks contributed a written law (the original Salic Law). The French had no written customs before the end of the reign of Charles VII (1461). The author has put his material in a convenient form for the student. It is carefully documented and indexed. To those biologists interested in race origins it will be a useful source book.

SAMUEL MARSDEN. *A Pioneer of Civilization in the South Seas.*

By S. M. Johnstone. Angus and Robertson, Sydney. 7s. 6d. 4¾ x 7¼; xiii + 256; 1932.

William Dampier landed on the west coast of Australia in 1688. Early in 1770 Cook landed on the southeastern coast at the spot that later became Botany Bay, though he called it Sting Ray Harbour. In August of the same year he formally took possession of the whole country in the name of the King, and called it New South Wales. During the period from 1776 to 1783, it will be recalled that England engaged in a controversy with her American colonies. At the end of the discussion one result was that America was no longer available as a parking place for English convicts. After due deliberation, and the rejection, for climatic reasons, of Africa

as a substitute, it was decided to use Cook's acquisition, New South Wales, for the purpose, and on May 13, 1787 the first batch of convicts (565 ♂ and 192 ♀) set sail from England.

Six years later Samuel Marsden went out to assist the chaplain of the colony and engage in missionary enterprises generally. He was then 29 years old, just ordained, and just married. The rest of his life was spent in Australia and New Zealand, except for visits home. He was a man of powerful personality and had a great influence in shaping the course of events in the early years of the two great British commonwealths of the southern hemisphere.

The student of human biology interested in the problems centering in what has been called the "clash of cultures" will find this book a mine of sound, well documented information. It is well indexed.

CONGORILLA. *Adventures with Pygmies and Gorillas in Africa.*

By Martin Johnson. Brewer, Warren and Putnam, New York. $3.50. $6\frac{1}{4}$ x $9\frac{1}{4}$; 281; 1932.

A mystery story could not be more exciting than this account of Mr. and Mrs. Martin Johnson's travels through the Belgian Congo. The pygmies of the Itura Forest become our intimate neighbors; the gorillas at least know man is about and a few become good friends when finally captured. It is interesting to note that the pygmies do not associate a picture as related to themselves in any way. Martin Johnson after having taken yards of film proposed entertaining his friends by evening movies. After it was over one asked: "When do we get paid?" and one wise little man upon being asked why he saw the same film three times replied: "I wanted to find out what you people saw in them." These people have more the minds of children and are childlike in their emotional life, their love being ruled more by friendly affection than passion. They are monogamous and once a wife is selected she is never deserted.

Johnson takes us into gorilla land and by his vivid writing we feel ourselves almost witnesses of probably the finest and most extensive exploring trip ever taken among the largest of apes in existence. It was estimated that there were at least 20,000 gorillas in the Alumbongo Range and this was only one territory. A few gorillas were caught, and this makes an exciting story in itself. Read this book and you will be thrilled, entertained and educated.

ALCOHOL AND MAN. *The Effects of Alcohol on Man in Health and Disease.*

Editor: Haven Emerson. Associate Editors: Henry A. Christian, Reid Hunt, Arthur Hunter, Charles C. Lieb, Walter R. Miles, Ernest G. Stillman. The Macmillan Co., New York. $3.50. 6 x $9\frac{1}{4}$; xi + 451; 1932.

At first glance this book would seem to be giving the average man who wants to know the real facts concerning alcohol a new deal. It has a distinguished list of editors and collaborators who have tackled the subject with vigor. Should one wish to learn of the effects of alcohol on human functions the first three chapters set forth selected ideas on the subject. The effects of alcohol on the cell and in heredity are rounded up in three more sections. Then alcohol as a poison and a medicine is discussed in the next two sections, the second of these consisting of papers by five physicians. Two chapters are devoted to alcohol and body resistance and pathology; three to the effect of alcohol on man's conduct and mentality; and three to alcohol and longevity, mortality and morbidity, with a final chapter on a review of recent literature on alcohol as a community health problem. By the time all of these various avenues have been traveled by the man "who wants to know" he will find himself emerging from the same old hole at which he entered. Too much alcohol is held to be always bad, no alcohol at all is generally approved of, though occasionally and somewhat grudgingly admitted to be not wholly desirable, and perhaps alcohol in moderate amounts is not always too bad. Each section contains a list of references. Figures and numerous tables explain the statistical data. The volume concludes with a glossary and

author index and a detailed subject index. The aridity of the editor is but ill-concealed.

A History of Ancient Mexico. 1547–1577.

By Fray Bernardino de Sahagun. Translated by Fanny R. Bandelier from the Spanish Version of Carlos Maria de Bustamante. Fisk University Press, Nashville, Tenn. $2.80. 6 x 9; ix + 315; 1932.

To Bernardino de Sahagun, a Franciscan monk, who went to Mexico in 1520 and remained there until his death in 1590, we are indebted for the first ethnological studies of ancient Mexicans. To Mrs. Bandelier, a student of early Spanish, we are indebted for this very able translation of the first part of Sahagun's history of twelve volumes from the Spanish version of Carlos Maria de Bustamante. More is to appear later. After a biographical sketch of the monk the sections of the volume are as follows: Book I, Prologue; The gods which ancient Mexicans adored; Book II, Feasts and sacrifices with which the natives honored their gods in the times of their paganism—Appendix to Book II; Book III, The origin of the gods—Appendix to Book III; and Book IV, About judicial astrology or art of divining which these Mexicans used in order to know which days were lucky and which were unlucky; about the fate of those who were born on days attributed to the marks or signs given below. It appears rather a matter of necromancy than of astrology. Mrs. Bandelier includes a bibliography of de Sahagun's works extracted from *Bibliografia Mexicana del Siglo XVI* by Señor Garcia Icazbalceta (Mexico, 1886). This is to be amplified in her second volume by additional data not now available. The work includes a foreword by Clark Wissler. There is an excellent index.

When the Scot Smiles *in Literature and Life.*

By A. H. Charteris. Alexander Maclehose and Co., London. 12s. 6d. $5\frac{1}{2}$ x $8\frac{3}{4}$; xiii + 304; 1932.

The author, formerly a solicitor in Glasgow, now living in New South Wales, where he is Professor of International Law in the University of Sydney, divides his book into three parts. In the first he analyses the characteristics of Scottish humor and traces it through prose and poetry from the time of William Dunbar (1465–1520) to modern times. As there are differences of character among the Scots due to place of birth, so are there differences of humor. It is all tinged, however, with a grim satire. The reason for this is

> surely to be found in the desperate poverty of Scotland which until long after the Union forbade urbanity, while the constant inculcation of strong moral doctrine—'the eternal verities' of the sage of Ecclefechan—permitted a humorous toying even with sacred things, only possible to those who are safely anchored in the faith.

In the second part of the book the author draws on his own recollections of Scottish humor in the Senate of the University, in the Law Courts, and in the city officers; the third part is from the papers of the late James Hamilton Muir concerning the adventures of "The Nipper" a typical pushing Scottish clerk. The book contains 16 illustrations, some of them very amusing. It is without an index.

Social Anthropology.

By Paul Radin. McGraw-Hill Book Co., New York. $3.50. $5\frac{3}{4}$ x 9; xii + 432; 1932.

The author of this book is lecturer in anthropology at the University of California. He has written, not for the professional anthropologist, but for "that vast array of students in economics, history, political science, jurisprudence, sociology and psychology who realize the bearing of social anthropology on their subject. . . . " He has kept his discussion free, except in the introductory chapter on the *History of Ethnological Theories*, from all general theoretical problems and has likewise avoided physical anthropology, archeology, linguistics and art. His problem is "the nature and range of primitive man's adjustment to his social needs and to the external world about him. How has he met the problems that have confronted man ever since he came into the world?" The

volume is divided into five main divisions as follows: The organization of the state; the organization of law and custom; the organization of economics and industrial life; religion and ritualism; and literature and mythology. The author does not limit himself to American tribes but uses all primitive peoples as the basis for his treatment. The work includes five maps showing tribe distribution, and a bibliography of 115 titles. It is well indexed.

Ethnographical Survey of the Miskito and Sumu Indians of Honduras and Nicaragua. *Smithsonian Institution, Bureau of American Ethnology Bulletin 106.*
By Eduard Conzemius. U. S. Government Printing Office, Washington. 25 cents. $5\frac{7}{8} \times 9$; vii + 191; 1932 (paper).

These two related tribes inhabit the larger part of the region known as the Mosquito Coast on the Atlantic side of Honduras and Nicaragua. The population of the Miskito tribe numbers about 15,000 at the present time, that of the Sumu about 3,000; and the author of this bulletin is of the opinion that the day of their complete disappearance or absorption by the Miskito tribe is not far off. Ever since the days of the buccaneers and early settlers the Miskito have assimilated all races, especially the negro, whereas the Sumu have mingled little with foreigners and remain a pure Indian tribe. This bulletin contains a mass of information concerning these two tribes; their physique, government and social organization, households, clothing, occupations, tools, amusements, music, hygiene, religion, marriage customs, burial customs, etc., past and present.

The Gold-Headed Cane.
By William Macmichael. Edited with Explanatory and Illustrative Notes and an Essay on William Macmichael, M.D., His Life, His Works, and His Editors, by Herbert S. Robinson. Froben Press, New York. \$3.50. 6 x 9; xxxi + 223; 1932.

The sixth edition of this delightful medicoliterary classic, first published in 1827, has been prepared with the intention of giving the reader, besides the original story of the Cane and its five masters, a biographical sketch of the author, William Macmichael; an account of his works, with bibliographical descriptions; specimens of Macmichael's handwriting, and separate portraits of himself, his wife, and their only child. The narrative as written by Macmichael contains many references which this editor has sought to annotate carefully as it is his conviction that

> a reference means little or nothing unless it is explained . . . . and that it is in every way better to find a note that one does not or may not need, than to need a note that one does not find.

Hence the book contains nearly 100 pages of notes and appendices. There is an index.

Niedersächsische Bauern. II. *Bevölkerungsbiologie der Elbinsel Finkenwärder vom dreissigjährigen Krieg bis zur Gegenwart.*
By Walter Scheidt. Gustav Fischer, Jena. 9 marks (paper); 10.50 marks (cloth). $6\frac{7}{8} \times 10\frac{1}{4}$; vi + 95 + folding table; 1932.

This monograph contains an analysis of biostatistical data found in the parish records of the island of Finkenwärder. The period covered most thoroughly extends from 1660 to 1870. The data consist of fairly complete protocols giving, for each individual who lived on the island during that time, the parentage, date of birth, dates and duration of marriage, number with dates of birth of offspring, occupations, date and cause of death, and other details. Theoretically, such data furnish excellent material for the study of certain problems of human biology and the author strongly recommends that modern statistical offices collect similar data. Practically, however, the labor of making the records is enormous and the results, as is well illustrated in this book, appear scarcely commensurate with the cost.

New Types of Old Americans at Harvard *and at Eastern Women's Colleges.*
By Gordon T. Bowles. Harvard University Press, Cambridge. \$2.50. $6\frac{1}{4} \times 9\frac{1}{2}$; xvi + 144; 1932.

Evidence for the presence of secular time trends of average dimensions of the adult human body continues to be derived from data recorded in the gymnasia and departments of physical education of American colleges. The principal material used in the book at hand consists of thirty different measurements on about 500 fathers and their sons, all of whom attended Harvard University between 1880 and 1917. There is also a similar series of measurements on approximately 500 mothers and daughters all of whom attended Smith, Vassar, Wellesley or Mt. Holyoke colleges. The results of the investigation are confirmatory of the now generally accepted conclusion that young adults in most civilized countries are taller, heavier, and in general larger than their parents of a generation ago. There is a short bibliography; the observational data are summarized by publication of means and standard deviations of frequency distributions. Space is given to correlation diagrams which might have been devoted more effectively to actual correlation tables.

Wetter und Krankheiten.
By Viktor Baar. Verlag "Ars Medici," Vienna. 3 schilling (paper); 4 schilling (cloth). 6 x 9; 171; 1932.

In an effort to trace the effect of various weather conditions on the onset and course of diseases (chiefly nasal, laryngeal, pulmonary and rheumatic) the author, who is chief city physician in Vienna, kept a daily weather report in addition to a record of the illnesses of his patients, over a period of eight years (1919–1926). Whenever more than three cases of a disease with a similar course occurred within two or three days, he looked on his weather chart to search for a contributory cause. His data, presented in diary form, together with monthly weather charts, take up the main bulk of the book. In an introduction he summarizes the diseases studied by months in which they were most prevalent (or, as in the case of tuberculosis, the months in which most deaths from that disease occurred). There is a short bibliography of German titles.

Our Children. *A Handbook for Parents. Edited by Dorothy Canfield Fisher and Sidonie Matsner Gruenberg. Prepared and Sponsored by the Child Study Association of America. Viking Press, New York.* \$2.75. $5\frac{1}{2}$ x $8\frac{1}{2}$; ix + 348; 1932.

A convenient handbook to which parents can turn to find the current thought about problems of child rearing. The twenty-nine contributing experts, all recognized authorities, cover adequately the fields of medical care, psychology, physiology, nutrition and school education. The book divides into four parts: (1) The growth and development of the child; (2) The child in the home; (3) The child in the school; and (4) The child in the outside world. Each chapter is prefaced by a list of typical parental questions which the expert writing the chapter may or may not answer, as in every case he has been allowed complete freedom in developing his subject.

Syllabus of Medical History.
By Victor Robinson. Froben Press, New York. \$1.00. $5\frac{7}{8}$ x 9; 110; 1932.

This syllabus, by the author of *The Story of Medicine* and *Pathfinders in Medicine*, consists of specimen questions and answers from his course in medical history, a specimen biographical essay on Duchenne of Boulogne from *Pathfinders in Medicine*, illustrations of primitive and Egyptian medicine, a specimen chronology of goiter, an article on The Photostat and its Value to Students of Medical History, by Charles Perry Fisher, a photostatic reproduction of an early text, and an index. Students in Robinson's course are surely fortunate in having so graphic and inspiring a teacher.

A Century of Public Health in Britain. 1832–1929.
By J. H. Harley Williams. A. and C. Black, London; The Macmillan Co., New York. 7s. 6d. net (England); \$2.50 (U. S. A.). $5\frac{1}{4}$ x $7\frac{3}{4}$; xv + 314; 1932.

It is recommended that this book be included in the collateral reading of students

of public health and preventive medicine, school medical officers, welfare workers, and all who are attracted by health problems. Beginning with the revolutionary and almost inhuman ideas of Edwin Chadwick the author traces in thoroughly readable fashion the progress of organized efforts to improve the public's health. Separate sections are devoted to antituberculosis work, child life and health, venereal disease control, and smallpox. The book closes with short biographical sketches of the "architects of social medicine," including Edwin Chadwick, John Simon, Florence Nightingale, Francis Galton, and Lord Shaftesbury. There is an adequate index.

MEDICAL ASPECTS OF OLD AGE. *Being a Revised and Enlarged Edition of the Linacre Lecture, 1922.*

By Sir Humphry Rolleston. The Macmillan Co., New York. $3.00. $5\frac{1}{8}$ x $7\frac{3}{4}$; ix + 205; 1932.

The material in this well-known book comprises a critical review of opinions which have prevailed at various times on the nature and cause of old age. This new edition contains much new material, and the discussion is brought up to date. It is a charmingly written, scholarly piece of work. There are indices of subjects and persons, and the book is thoroughly documented.

AMERICAN POPULATION BEFORE THE FEDERAL CENSUS OF 1790.

By Evarts B. Greene and Virginia D. Harrington. Columbia University Press, New York. $3.50. 6 x 9; xxiii + 228; 1932.

This source book brings together in a single volume much material not easily accessible to the student of population. This includes estimates, censuses, and partial enumerations, such as number of militia, polls, taxables, or families, for the thirteen colonies as a whole, and for each state and its local subdivisions. The value of the book is enhanced by a bibliography of twelve pages and an index.

THE ILLEGALLY EMPLOYED MINOR AND THE WORKMEN'S COMPENSATION LAW. *U. S. Department of Labor, Children's Bureau Publication No. 214.*

By Ellen N. Matthews. U. S. Government Printing Office, Washington. 15 cents. $5\frac{3}{4}$ x 9; v + 225; 1932 (paper).

This inquiry is primarily concerned with the workmen's compensation laws as they affect the illegally employed minor, in two states, Wisconsin and Indiana. In the former the youngster injured while working in industries prohibited to him by law is covered by the state Workmen's Compensation Act, and in addition is entitled to extra compensation based upon his probable earning capacity at his majority. In Indiana he is excluded from the Act but may sue at common law.

HARMONIOUS DEVELOPMENT OF WOMEN'S BODIES.

By Alice Bloch. Translated from the Sixth German Edition by Mathias H. Macherey. Ray Long and Richard R. Smith, New York. $3.00. 7 x 10; x + 136 + 13 pages illustrations; 1932.

A rational attitude towards gymnastics is herein expressed. The purpose of exercise, the author states, is to develop a beautiful and graceful body, hence she cautions one to take time in learning the exercises, and not to overdo. The chapter on posture and breathing exercises is especially sound. There is a section of beautiful illustrations of nude figures, to serve as a guide towards performing the exercises correctly. There is no index.

EMPLOYED BOYS AND GIRLS IN MILWAUKEE. *U. S. Department of Labor, Children's Bureau Publication No. 213.*

By Alice Channing. U. S. Government Printing Office, Washington. 10 cents. $5\frac{3}{4}$ x $8\frac{3}{4}$; v + 71; 1932 (paper).

FACTS ABOUT JUVENILE DELINQUENCY. *Its Prevention and Treatment. U. S. Department of Labor, Children's Bureau Publication No. 215.*

U. S. Government Printing Office, Washington. 10 cents. $5\frac{7}{8}$ x $9\frac{1}{8}$; iv + 44; 1932 (paper).

ZOÖLOGY

PHYSIOLOGY OF THE TEMPERATURE OF BIRDS. *Scientific Publications of the Cleveland Museum of Natural History, Vol. III. Contribution No. 21 from The Baldwin Bird Research Laboratory, Gates Mills, Ohio.*

By S. Prentiss Baldwin and S. Charles Kendeigh. Cleveland Museum of Natural History, Cleveland. \$2.20 (paper); \$2.85 (cloth). $6\frac{1}{4} \times 9\frac{1}{4}$; x + 196; 1932.

This publication includes experimental studies, carried out under controlled conditions, to determine the factors affecting avian temperature, and studies of the way in which these factors affect the bird under natural conditions. Most of the work was performed on the eastern house wren, *Troglodytes aedon aedon*. The body temperature of birds at standard metabolism, 104.4°F., was used as a basis for comparing the influence of various factors. Among those found to stimulate the amount of heat produced are: emotional excitement, muscular activity, food, extreme changes of air temperature, and attentiveness on the part of the adult female when incubating eggs. The lower and upper lethal limits of body temperature are 71.0°F. and 116.3° F., respectively.

The body temperature of nestling birds, and the temperature of the eggs and nest are also investigated. The temperature of young birds in the nest, before development of a temperature control, varies directly with that of the nest. During the period in the nest there is a gradual rise of body temperature independent of environmental conditions and dependent upon the development of the temperature regulating mechanism. This rise amounts to 0.6°F. per day. Egg temperature under experimental control varies directly and rapidly with air temperature.

A bibliography is included, comprising all the important papers having a direct bearing upon the physiology of temperature in birds, and there is a full index.

WILD LIFE COMMISSION OF MALAYA. *Report of the Wild Life Commission. Volume I—General Survey. Volume II—Recommendations. Vol. III—Malayan Enactments, Extracts from Laws of Other Countries, etc.*

Government Printing Office, Singapore. \$4.00 per volume. $6 \times 9\frac{3}{8}$; Vol. I, 421 + vii; Vol. II, 289 + ix + 29 plates + 2 folding maps; Vol. III, 379; 1932 (paper).

This report of the Wild Life Commission for the Malay States and the Straits Settlements comes at an opportune moment, for there is probably no part of the British empire where less attempt has been made to preserve the native fauna. Up to now, there has been very little protectionist sentiment in that part of the world, and the exploitation of large areas for rubber plantations has resulted in an attitude distinctly hostile to preservation.

Mr. Hubback has made a valuable contribution to the literature of conservation in this report on an area of some 53,000 square miles. Not only does the commission critically examine the present state of affairs, but also offers constructive remedies in the shape of draft enactments complete down to the last detail of game department organization and creation of a self-maintaining game fund. These proposed plans are based on a world-wide knowledge of game laws. It seems to us that any legislative body should be sufficiently impressed by the breadth of technical and practical knowledge displayed to confirm the recommendations of the commission without too much modification. The survey was completed in eight months, in the course of which the two investigators covered some 7,300 miles. The cost of the survey, including printing the report, was \$11,000 (a Straits dollar is worth 2/4).

It seems noteworthy that a small, relatively undeveloped country such as Malaya should invest in such a survey of its wild life resources with a view to their preservation and more efficient utilization.

THE VERTEBRAL COLUMNS OF RICOCHETAL RODENTS. *Bulletin of the American Museum of Natural History, Volume LXIII, 1932, Article VI.*

By Robert T. Hatt. American Museum of Natural History, New York. \$1.65. $6\frac{1}{4} \times 9\frac{3}{4}$; 139 + 10 plates; 1932 (paper).

Approximately 60 specimens, belonging to

over 40 different genera (8 families), furnish the basis for quantitative and qualitative comparisons of the skeletal characteristics of ricochetal rodents. The introduction contains a concise discussion of related modes of locomotion and the ricochet is defined as

"Forward progression by a series of rebounds in which the two hind feet strike the ground at the same moment and practically synchronously, and the fore feet not at all. This is rapid, sustained hopping." (p. 602). Although it is stated that "ricochetal rodents have their vertebral columns modified from the primitive quadrupedal type more for the changed mechanical conditions consequent to bipedalism and the ricochet, than for other activities," (p. 702).

great variation is introduced by "other activities." Morphological characteristics, which are definitely correlated with the type of locomotion, will require a good deal more study of many more cases than were available for this report. There is a bibliography of 151 titles; ten plates illustrate various characteristics of the ricochetal types; twenty-three pages are devoted to tables which indicate that percentages and ratios are still favorite modes of expressing observational data.

THRILLS OF A NATURALIST'S QUEST.
By Raymond L. Ditmars. The Macmillan Co., New York. $3.50. $5\frac{7}{8}$ x $8\frac{3}{4}$; xii + 268; 1932.

Two features make this book different from most scientists' reminiscences. Ditmars learned to write smoothly and colloquially while working as a reporter, and he learned about snakes in spite of anything anyone could do about it. The former accomplishment has given him the ability to set down his observations about snakes, and himself, in an unaffected way, and the second provided him with the groundwork of his narratives. He collected poisonous snakes as a boy and kept them in his bedroom, not without memorable incident, and studied snakes under natural conditions in both Americas, and in captivity in the zoo and in the circus. Interesting observations on the habits of snakes and of captive animals in general are scattered all through the book. A great many of his activities in collecting, feeding, and transporting snakes to the zoo had to be done surreptitiously and often this resulted in amusing incidents. It strikes us that almost anyone interested in nature, from a twelve year old Girl Scout to an emeritus professor ought to find this an entertaining account of the life and doings of a wide-awake naturalist.

MEDICAL ENTOMOLOGY.
By Robert Matheson. Charles C Thomas, Springfield, Ill. $5.00. $6\frac{1}{4}$ x $9\frac{1}{4}$; xiii + 489; 1932.

This scholarly work opens with a brief historical account of the great leaders in medical entomology. The author then proceeds to discuss the various orders of arthropods and their bearing on human disease. The book is designed essentially as an introduction for the student, physician, public-health man, entomologist and layman. It is written in textbook form and limited in scope, in general, to a classification and description of each insect discussed, its effect on man, its occurrence in nature, and possible means for its extermination. A great deal of sound advice about dealing with insects is given. Each chapter is provided with a selected bibliography.

THE COPEPODS OF THE WOODS HOLE REGION, MASSACHUSETTS. *Smithsonian Institution, United States National Museum Bulletin 158.*
By Charles B. Wilson. U. S. Government Printing Office, Washington. 75 cents. $6\frac{1}{4}$ x $9\frac{3}{4}$; xix + 635 + 41 plates; 1932 (paper).

This report, which comprises a study of marine, brackish-water, and fresh-water copepods—free-swimming, commensal, semiparasitic, and parasitic species—is based largely on the collection made by the late Dr. Richard Rathbun from 1881 to 1885, together with collections made by the author. The descriptions pay especial attention to the living coloration of the species. As a result of the use of trawl wings in dredging and of the examination of ponds and sand beaches many species never before reported from the Woods Hole

region have been found. Keys are included as an aid in identification; the keys to the genera include practically every valid genus thus far described; the keys to the species include only those found in the region. There are bibliographic references to the species and an index.

ECONOMIC MAMMALOGY.
By Junius Henderson and Elberta L. Craig. Charles C Thomas, Springfield, Ill. \$4.50 postpaid. $6\frac{3}{8} \times 9\frac{1}{4}$; x + 397; 1932.

Since the literature on economic mammalogy has been scattered extensively through a large number of periodicals, an attempt to condense this information into a book is justified. The book is well written in the textbook form and should be a useful introduction for students. Among the subjects considered are the economic relations of mammals; their direct and indirect influence on humanity; their food habits; methods of preserving and increasing those species of use and benefit to man, and the control of harmful mammals. There is an extensive bibliography and an index.

FOODS OF SOME PREDATORY FUR-BEARING ANIMALS IN MICHIGAN. *University of Michigan, School of Forestry and Conservation Bulletin No. 1.*
By Ned Dearborn. University of Michigan Press, Ann Arbor. 25 cents. 6 x 9; 52; 1932 (paper).

The results of an investigation on the food habits of the raccoon, opossum, red fox, coyote, wild cat, skunk, mink, weasel and badger, based on examinations of stomach contents and residues in the feces.

MY SWANS. *The Wylly-Wyllys and Others.*
By E. L. Turner. J. W. Arrowsmith, London. 3s. 6d. $5\frac{1}{2} \times 7\frac{1}{8}$; 126; 1932.

We find comparatively few people interested in these beautiful birds and seldom any possessing such intimate knowledge of their thought and life as our author. The illustrations are splendid, the account is short and attractively written.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XXII.*
Edited by G. Grimpe and E. Wagler. Akademische Verlagsgesellschaft, Leipzig. 13.60 marks. 6 x $8\frac{1}{2}$; 152; 1932 (paper).

In this installment of an excellent survey of the fauna of the North and Baltic seas, previous numbers of which have been reviewed in these columns, the following groups are dealt with: Archiannelida, by A. Remane; Phoronidea, by Carl I. Cori; Euphausiacea, by C. Zimmer; Cetacea, by L. Freund. Each section is furnished with a bibliography.

REMARKS ON THE AFFINITIES OF THE MAMMALIAN FAUNA OF VANCOUVER ISLAND, BRITISH COLUMBIA, WITH DESCRIPTIONS OF NEW SUBSPECIES. *University of California Publications in Zoology, Volume 38, No. 12.*
By E. Raymond Hall. University of California Press, Berkeley. 25 cents. $7\frac{1}{8} \times 10\frac{3}{4}$; 11; 1932 (paper).

BOTANY

WILD FLOWERS OF THE ALLEGHANIES. *Being a Description of Their Character, Habits, Flowering Season, and Location; a Concise Definition of Colors, References to Medicinal Properties, Notations of the Insects that Assist in Their Fertilization; also Numerous Flower Legends, Historical References and a Fully Illustrated Key to the Most Important Diagnostic Characters of the Families Represented. A Check List of Ferns Occurring in the Area is Appended.*
By Joseph E. Harned. Joseph E. Harned, Oakland, Md. \$4.50. $5\frac{3}{8} \times 8$; xxxii + 670; 1931.

FLOWERS OF GRASS. *How to Know the Names of the British Grasses. A Handbook for Beginners.*
By Robert Fisher. Wheldon and Wesley, London. 2 shillings. 5 x $7\frac{1}{4}$; 47 + 11 plates; 1932.

There is no reason why more botanical manuals of the type of *Wild Flowers of the Alleghanies* should not be written for nature lovers and for beginners to whom the standard taxonomic books are appalling. Harned's book is a thoroughly respectable

key to the ferns and flowering plants of the Alleghany Mountains from Canada to the northern part of Alabama written by a man who takes pleasure in studying nature. It is beautifully illustrated with large and accurate drawings, colored plates, and a few first-rate photographs, but it is not in any sense the usual picture-book kind of flower manual. It aims to tell something about plants besides their names; bits of mythology from antiquity and folklore from the Americas; the kind of remarks an observant field naturalist would set down; and whatever features of plants struck the author's fancy. He is not only religious, but devout, there is no mistaking that. In spite of that we are bound to admit that he seems to have the knack of teaching science to young people, and to amateurs in general, as few people have.

The manual of the British grasses is intended for beginning botanists, and as this is by no means an easy group of plants to study, it has nearly 30 illustrations designed to show the structure of grasses and their flowers. Perhaps the illustrations and the studied simplicity of the analytical key should make it useful to American amateur botanists as a supplement to the usual taxonomic manuals, as many species are common to the British Isles and to the region covered by Gray's Manual.

Men of the Trees. *In the Mahogany Forests of Kenya and Nigeria.*

By Richard St. Barbe Baker. The Dial Press, New York. $5.00. $6\frac{1}{4} \times 9\frac{1}{8}$; 283; 1931.

The material for this book stems from the author's experience as Assistant Conservator of Forests in Kenya and Nigeria. In spite of the fact that it is replete with the kind of enthusiastic uplifting goodness that would be expected to trickle stickily from a pot in which Pollyanna and a Boy Scout had been boiled down together, the book does contain a considerable amount of useful and interesting information, and a lot of superb photographs. Both the ecologist and the anthropologist will find material in it. Tropical forests are shown not to be inexhaustible. The wrong kind of exploitation can easily wipe them out. The author's chief missionary concern is to insert this idea into the native's head, and at the same time teach him how to manage his forests so that hopefully he will still have the kind of dwelling place to which he is attached, even after the white man has taken his loot from the green gold of the forest. Apparently he has been rather successful in this enterprise. The book has no index.

Root Nodule Bacteria and Leguminous Plants. *University of Wisconsin Studies in Science Number 5.*

By Edwin B. Fred, Ira L. Baldwin, Elizabeth McCoy. University of Wisconsin, Madison. $3.00. $7\frac{1}{8} \times 10\frac{5}{8}$; xxii + 343; 1932 (paper).

This is a well written critical review of the literature on the symbiotic bacteria associated with leguminous plants. Root nodules were first figured by Fuchs in 1542 and since then a great amount has been written on several phases of the problem. The subject as it is treated here should be of interest to several kinds of scientific workers. Bacteriologists will find a considerable portion of the monograph devoted to the cultural characteristics of the bacteria and their relation to nitrogen in the plant and on culture media. The treatment of the development and histology of nodules of bacterial origin in leguminous plants and in a few other species falls within the range of interest of botanists, as should also three or four pages on some plants whose nodules are in the leaves. Agronomists will find a good deal of space devoted to methods of inoculation and to the economics of the method. There are nearly fifty full page plates, judiciously chosen, numerous tables, an index, and more than a thousand bibliographical citations, to supplement the text.

Contribution à l'Étude Écologique des Blés de la Region du Rhone Moyen (Drôme-Ardèche).

By A. Dusseau. Office Régional Agricole du Midi, Marseille. $6 \times 9\frac{1}{2}$; 214; 1932 (paper).

Throughout France the baking quality of wheat depends in high degree upon the locality in which it is grown, but fortunately for the French farmer the tastes in bread vary just as much, and almost every grade of wheat is specially esteemed somewhere. This variation has prompted a taxonomic study of wheat varieties on a biometric basis, the ecological conditions under which they are grown, and the quality of flour they yield. Mlle. Dusseau's report on the Puy-de-Dôme was reviewed in an earlier issue of The Quarterly Review of Biology; this bulletin concerns the departments Drôme and Ardèche. In these papers, which are in large part summaries of official statistics, she has been able to leave the charts showing soil types and distributions of arable lands and crop yields relatively free from unneeded lettering by the simple device of providing maps printed on celluloid bearing the names of cantons and rivers which may be superimposed on the charts.

Der Formwechsel der Pennaten Diatomeen (Kieselalgen).

By Lothar Geitler. Gustav Fischer, Jena. 20 marks. $6\frac{1}{4}$ x 9; 226; 1932 (paper).

Diatoms have an interesting life cycle

which begins with the auxospore, continues in the vegetative division of the cells with progressive reduction in size and is terminated by the production of auxospore mother cells and auxospores which is generally connected with sexuality. Small cells in which auxospore production is suppressed continue to divide with progressive reduction in size until a certain minimal size is reached. Such cells cannot re-enter the developmental cycle but die off.

In the normal life cycle, diminution in size is accompanied by alterations in the proportions of the cells, for the most part due to a lessening of the relative length of the apical axis. This alteration in form has been traced through the developmental cycles of a number of diatom species. The bibliography has more than 150 titles.

Some Aspects of Plant Nutrition.

By B. Viswa Nath. Society of Biological Chemists, Bangalore, India. Re. 1. $5\frac{1}{2}$ x $8\frac{1}{2}$; 39; 1932 (paper).

This little review begins with the remark that "between the years 2500 B.C. and 500 A.D. the knowledge of soils and plants possessed by ancient India was at a high standard of level, approaching modern views and practices in many respects. For ten centuries after the year 500 A.D. the trail of progress of agriculture is lost." In order to bring Indian agronomists up to date again in knowledge of soil management Mr. Nath has prepared a very good review of about 150 papers on soil science and plant physiology, emphasizing the interrelationships of soil, plants, and animals. Unlike American experiment station bulletins, this ends on a philosophic level with a passage on the essential unity of life and the balance of Nature.

Respiration in Plants.

By Walter Stiles and William Leach. The Dial Press, New York. \$1.50. $4\frac{1}{8}$ x $6\frac{1}{2}$; vii + 124; 1932.

The purpose of this book is to give "an account of the nature of plant respiration which is readable and understandable by the elementary student of botany and which at the same time contains sufficient information to render it of value to the advanced student." Both kinds of students, and physiologists in general, will find this a very useful survey of a heterogeneous subject in which the experimental work is of very uneven quality. The method is to discuss a limited number of researches that illustrate the more important principles of plant respiration, closing with a chapter on recent theories of the chemical mechanism of respiration. There is a bibliography of about 120 titles and a usable index.

Alcoholic Fermentation.

By Arthur Harden. Longmans, Green and Co., New York. \$5.50. 6 x $9\frac{5}{8}$; vii + 243; 1932.

This is the fourth edition of a standard monograph on the mode of action of the enzymes concerned in the fermentation of sugars by yeast. It does not consider the physiology of the growing yeast cell at

any length but is confined for the most part to the properties of the yeast juices and the chemical changes they induce. There is a very well written historical introduction, covering 17 pages. Compared with the third edition the number of citations has been nearly doubled and amounts to a little less than a thousand. It is provided with an excellent index.

MORPHOLOGY

LEHRBUCH DER HISTOLOGIE UND HISTOGENESE. *Dritte, Neubearbeitete Auflage.*
By Josef Schaffer. Wilhelm Engelmann, Leipzig. 18 marks (paper); 20 marks (cloth). $6\frac{5}{8}$ x $9\frac{3}{4}$; viii + 576; 1933.

Part I of this excellent text treats of the simple tissues; Part II of the histology of organs and glands. The second edition was published ten years ago and the author has revised it page by page to bring this third edition up-to-date. The embryonic development of the lattice fibres, supporting tissues, the construction of the neuroglia, the smooth muscle fibres of the alveoli of the lungs, and the placenta are treated in greater detail. The section on glands has been entirely rewritten, and the physiological and biological aspects as well as the morphological are discussed. A bibliography of 26 pages has been added. An adequate index, over 600 excellent text figures, and 14 colored plates further enhance the value of this book, which is altogether an outstanding textbook.

A MANUAL OF EMBRYOLOGY. *The Development of the Human Body.*
By J. Ernest Frazer. William Wood & Co., Baltimore. $8.00 net. $6\frac{1}{4}$ x $9\frac{1}{4}$; viii + 486; 1932.

The regional method is employed in this book in describing the development of the human embryo. The subject is dealt with in two parts. In Part I, the early and general development of the embryo is considered, and in Part II, the development of organs and regions. New descriptions, derived by the author in working out on human material the processes of development, are incorporated. No references are included, except that when a statement is made on the authority of some other worker the name is put in brackets. There is a full index.

GRUNDZÜGE DER ENTWICKLUNGSGESCHICHTE DES MENSCHEN IN VERGLEICHENDER DARSTELLUNG. 13., *neubearbeitete Auflage.*
By Richard Weissenberg. Georg Thieme, Leipzig. 13.50 marks. 5 x $7\frac{3}{4}$; xviii + 448 + 5 plates; 1933.

In addition to having undergone another revision as to text—notably in the sections on the development of the circulatory system of the liver and the development of the brain—this standard handbook of embryology has been considerably dressed up as to format. This edition is printed on a high-grade quality of paper which enhances the text figures, and a number of new figures have been added or substituted.

PHYSIOLOGY AND PATHOLOGY

THE MECHANISM OF NERVOUS ACTION. *Electrical Studies of the Neurone.*
By E. D. Adrian. University of Pennsylvania Press, Philadelphia. $2.00. 6 x 9; x + 103; 1932.

This work is primarily concerned with the behavior of the units which make up the nervous system, as determined with the aid of the vacuum tube amplifier. The best results, to date, have come from the peripheral nerves. When a nerve is stimulated electrically, it is found that the potential change in each fibre is of fixed magnitude and duration, and that it depends only on the state of the fibre and not on the strength of the stimulus which set it in motion. The activity of the sensory nerve fibres in transmitting messages to the central nervous system seems to consist merely of a series of brief impulses or waves following one another more or less closely. In any one fibre the waves are all of the same form. The same kind of electrical activity is found in the motor nerve fibres. The impulses in the sympathetic system and in the smallest sensory fibres are conducted much more slowly than those in the

large motor and sensory fibres, but there is no evidence that any other kind of activity is present than that involved in the conduction of impulses. The same kind of activity is found in nerve fibres from all sorts of animals.

The action of the sense organs is then considered. Variations in excitability and in adaptation rate are the chief differences which can be observed in the reactions of the sense organs which respond to mechanical stimulation. The work of Wever and Bray on the auditory nerve is discussed, and the conclusion drawn that with the auditory as with the tactile nerve fibres the intensity of the stimulus is judged by the number of impulses making up each volley.

A chapter is devoted to the pain mechanism. The main problem is that of the specific effects of different sensory fibres. Increase of stimulus is known to cause more intense pain. The question arises as to whether pain is due to a very high frequency of discharge, or whether it is due to nerve fibres which can give rise to no other sensation. From data obtained from work on the frog and on mammals it is concluded that it is unlikely that pain is always due to specific pain fibres.

> It may be nearer the mark to say that the sensation produced by nerve fibres of a given type becomes a closer and closer approach to pure pain in proportion to the slowness of conduction of the fibre and the lack of sensitivity in the end organ. The most sensitive tactile endings and their rapid nerve fibres cannot cause pain: the slow non-medullated fibres with their endings which respond only to noxious stimuli can cause little else, but for all we know the smaller medullated fibres may give both contact or pain according to the magnitude of the discharge.

Discharges in motor fibres are then considered, and in the final chapter, the activity of nerve cells. In closing, the author states:

> All conclusions about the central nervous system must be tentative, and the conclusion of this work is little more than a restatement of the cellular hypothesis. The nervous system is built up out of specialised cells whose reactions do not differ fundamentally from one another or from the reactions of the other kinds of excitable cell. They have a fairly simple mechanism when we treat them as individuals: their behaviour in the mass may be quite another story, but this is for future work to decide.

The book contains a bibliography and is indexed.

HEARING IN MAN AND ANIMALS.

By R. T. Beatty. G. Bell and Sons, London. 12 shillings net. $5\frac{1}{2} \times 8\frac{3}{4}$; xi + 227; 1932.

A fascinating description of the nature of the various mechanisms by which animals, from insect to man, hear, and the evolution of these mechanisms. The book is primarily designed for the general reader, but it will also be instructive to biologists unfamiliar with its specialized field. The author has collected and correlated data from the fields of anatomy, physiology, physics, acoustic engineering and psychology and has written down this information with as little use of technical terms as possible.

The first chapter, which gives a detailed description of the human ear and the functions of its various parts, is followed by a discussion of the evolution of the ear, beginning with the primitive auditory mechanisms of fishes. A chapter each is devoted to the resonance and non-resonance theories of hearing. The chapter devoted to hearing in animals contains some interesting facts and explodes some time-honored beliefs. Fish, we learn, cannot hear air-borne sounds, so the fisherman need no longer heed Isaac Walton's advice, but may talk to his heart's content without fear of lessening his catch.. Snakes, likewise, are insusceptible to air-borne sounds, and react to the charmer's motions rather than to his piping. Other material is concerned with brain and nerve mechanisms involved in the process of hearing; music; noises; and defects in hearing. References are listed at the end of each chapter, and an index has been provided.

SOME FACTORS IN THE LOCALISATION OF DISEASE IN THE BODY.

By Harold Burrows. William Wood & Co., Baltimore. \$4.50. $5\frac{3}{8} \times 8\frac{1}{2}$; xi + 299; 1932.

This book is divided into three parts. Part I deals with localisation from the bloodstream of colloidal and other matters and includes chapters on the localisation of normal and foreign proteins, of dyes and fine inorganic particles, of syphi-

lis, bacteria, viruses and cancer. In Part II factors in localisation are considered. Part III is devoted to a general discussion of the phenomenon of localisation. The conclusion is that

> Three conditions are required for the localisation of many blood-borne diseases—namely:
> (1) An abnormal permeability of the walls of the small blood vessels.
> (2) The presence of forces which will transport the noxious agents through the endothelial cytoplasm.
> (3) The retention of noxious agents in the tissues under the influence of inflammation.
> The three conditions mentioned above lead to the localisation, not only of the agents of disease, but to the factors of defence.

There is a full bibliography and an index.

FADS AND QUACKERY IN HEALING. *An Analysis of the Foibles of the Healing Cults, with Essays on Various Other Peculiar Notions in the Health Field.*

By Morris Fishbein. Covici, Friede, New York. \$3.50. $5\frac{1}{2} \times 8\frac{1}{2}$; vii + 384; 1932.

The thing that distinguishes this book from most protests against medical quacks and fraudulent health treatments is that Doctor Fishbein's indignation is usually mixed with amusement, not malicious humor or irony, but a good-natured appreciation of the ridiculous. For instance, after dealing with chiropractic according to its deserts he is able to say

> Most of the patients of chiropractors are women. An old farmer down in Kansas said that he had noticed that whenever a man came to a chiropractor, the bone in his spine that was out of place was usually near the head. The idea offers intriguing possibilities for continued thought.

This sort of thing not only makes interesting reading, and there is page after page of it, but it impresses us as being an uncommonly good means of combatting the quacks. Christian Science, osteopathy, the Abrams box, and a host of health cults with fancy names, come in for some rough treatment, along with muscle builders and beauticians; in fact, in one sense it is an annotated catalogue of the more conspicuous individuals or groups who have competed or interfered with scientific medicine in this country since colonial times. It has a useful index.

A GUIDE TO HUMAN PARASITOLOGY *for Medical Practitioners.*

By D. B. Blacklock and T. Southwell. William Wood and Co., Baltimore. \$4.00 net. $5\frac{7}{8} \times 9\frac{3}{8}$; viii + 271; 1932.

This book is intended for the practitioner who has had no experience in parasitology. Emphasis is laid only on the pathogenic organisms, and descriptions are restricted to those characters in them which are of immediate diagnostic value. The technique of using a microscope and of examing material is outlined, after which the parasites are systematically described. Eleven tables deal with the relation of parasites to food and water, different vehicles in the spread of parasitic diseases, the diagnostic features of parasites, and other matters. Mention is made of some of the drugs of use in the treatment of the different diseases. A list of larger text books is given and there is an index.

PROTOPLASMIC ACTION AND NERVOUS ACTION. *Second Edition.*

By Ralph S. Lillie. University of Chicago Press, Chicago. \$3.00. $5 \times 7\frac{1}{2}$; xiii + 417; 1932.

The subject matter of this book, widely and favorably known in its first edition, is concerned with the fundamental biological problems of vital organization, growth and development.

> The structural and physico-chemical organization of living matter, the modifiability of its rate of reaction under varying conditions (irritability), and its transmissive property (so highly developed in nervous tissues) are considered in some detail; and their probable relation to the polyphasic and film-partitioned character of the protoplasmic system is indicated.

Previous experimental work in the field is summarized and the author's own studies are included. The book is well documented, and there is an index. The changes and additions in the second edition are not great, and are only for the purpose of bringing the discussion up to date.

PHYSIOLOGY OF FARM ANIMALS.

By F. H. A. Marshall and E. T. Halnan. The Macmillan Co., New York. \$3.25. $5\frac{1}{2} \times 8\frac{5}{8}$; xiv + 366; 1932.

A book which covers successfully a field of physiology hitherto neglected, and certainly of economic importance. There is a great deal of valuable information for the stock breeder, though the book is written primarily as a textbook for students of agriculture. The first part of the book, after a brief discussion of histology and chemistry of foods, devotes a chapter to each of the organ systems. The last part gives a survey of present knowledge of the growth and nutrition of farm animals.

VISION AND COLOUR VISION.

By R. A. Houstoun. Longmans, Green and Co., New York. \$4.50. $5\frac{3}{8} \times 8\frac{1}{2}$; vii + 238; 1932.

An extensive discussion of vision from the physical, physiological, and psychological standpoints, with rather more emphasis on the physical side. The author, however, deals with the multiplicity of factors concerned in the phenomenon of color vision in a logical and thoroughly sound manner. The book embodies the most recent work on vision, most of which has not yet been put into the textbooks. There is an interesting discussion of the Young-Helmholtz theory of color vision, pointing out some of its logical weaknesses.

A TEXTBOOK OF GENERAL PHYSIOLOGY *for Colleges.*

By Philip H. Mitchell. McGraw-Hill Book Co., New York. \$6.00. $5\frac{7}{8} \times 9$; xviii + 799; 1932.

This is the second edition of an excellent general physiology textbook designed for students whose training in physical chemistry and biochemistry is meager.

In addition to the general revision, the second edition differs radically from the first in two respects:

1. Much less space has been given to the biochemical aspects of physiology in order to make room for more physical chemistry as applied to physiology. To this end, several of the earlier chapters have been eliminated or condensed and four entirely new ones, Surface Action, The Colloidal State, Diffusion and Osmosis, and The Permeability of Cells, have been added.
2. The general arrangement of the subject matter as indicated by the new order of chapters has been changed to conform with what seems to be the more general and convenient practice among teachers of general physiology.

VETERINARY PATHOLOGY AND BACTERIOLOGY.

By S. H. Gaiger and Gwilym O. Davies. Alex. Eger, Chicago. \$6.50. $5\frac{3}{8} \times 8\frac{3}{8}$; viii + 610; 1932.

The outstanding feature of this textbook is its photographic illustrations, mostly from original specimens in the Museum of the Department of Animal Pathology in the University of Liverpool. These are numerous and excellent. The text is organized on a subject basis. Pathology, bacteriology, virus infections, protozoology and mycology as found in animal diseases are concisely but well treated. This is a sound and useful text, well indexed.

THE PRINCIPLES OF OPTICS.

By Arthur C. Hardy and Fred H. Perrin. McGraw-Hill Book Co., New York. \$6.00. $5\frac{3}{4} \times 9$; xiii + 632; 1932.

This textbook of optics ought to be welcomed by biologists because of the care taken to describe the kinds of optical equipment which find application in biological work, and to discuss the principles of their operation. The chapters on light sources, photography, light-sensitive cells, and microscopes, should be particularly useful to biologists. There are numerous references to more technical treatments of particular topics, and there is an excellent index.

RECHERCHES SUR L'INFECTION, L'HYPERSENSIBILITÉ ET L'IMMUNITÉ *vis-à-vis des Formes Virulentes ou Atténuées du Virus Tuberculeux.*

By Jean van Beneden. Masson et Cie, Paris. 25 francs. $5\frac{1}{2} \times 8\frac{7}{8}$; 135; 1932 (paper).

A description of important experiments conducted by the author in the Laboratories of Bacteriology and Hygiene of the University of Liège, bearing on the filtrable element of the tubercular virus and on the attenuated stock of Calmette and Guérin

(BCG). The purpose was to differentiate diverse reactions of infections, hypersensibility to tuberculin, hypersensibility to superinfection, and immunity. The author believes that the differences which these experiments have established between certain reactions will facilitate an understanding of the close connection between various phenomena concerned in the acquisition of resistance to tubercular infection. The book is equipped with a bibliography on BCG and ultra-virus, and an author index.

Introduction à la Chirurgie Nerveuse. *By E. E. Lauwers. Masson et Cie, Paris.* 25 francs. $6\frac{1}{4}$ x $9\frac{1}{4}$; vii + 121; 1932 (paper).

A résumé, written primarily for the use of the neural surgeon, of the important researches made in recent years concerning the physiology and pathology of the nervous system. The various chapters treat of the meninges and the cerebrospinal fluid, encephalon, spinal marrow, peripheral nerves, and the sympathetic nervous system. The book lacks an index and a systematic bibliography, although some references—a total of 82—are given as footnotes.

Health Departments of States and Provinces of the United States and Canada. *Public Health Bulletin No. 184 (Revised).* *Compiled by John A. Ferrell, Wilson G. Smillie, Platt W. Covington, Pauline A. Mead. U. S. Government Printing Office, Washington.* 75 cents. $5\frac{3}{4}$ x $9\frac{1}{8}$; vi + 785; 1932 (paper).

An extensive and useful summary of official public health organizations in each of the states and provinces of the United States and Canada. The compilation is thoroughly done and furnishes a valuable source for reference.

Cancer and Sarcoma One; Identical in Cytology. *Finding the Pure Cancer Cytology, Only, in a Reported Case of Undifferentiated Round Cell Sarcoma; Revision of Many Cases of Sarcoma Yield Pure Carcinoma on Restudy. Does "Cure of Cancer" 10–18 Years, Post Operation with no Recurrences, Then Fatal Recurrences, Suggest a Dormant Abeyant Chronic Form of Cancer—a Benign Form of Cancer? Various (30) Cases in Point of Discussion. The Causal Diminutive Cancer Cellulettes, Dormant or Active, Must be Neutralized or Destroyed for Ultimate Cure. A Further Amplification of the Specific Cancer Cellule and Its Conduct. Transmutation. Cell Division.* *By Frank A. Stahl. Frank A. Stahl, Hamilton Club, Chicago.* Edition limited complimentary. 6 x $9\frac{1}{8}$; 60; 1932 (paper).

BIOCHEMISTRY

On the Mechanism of Oxidation. *By Heinrich Wieland. Yale University Press, New Haven.* \$2.50. $5\frac{7}{8}$ x $9\frac{1}{8}$; x + 121; 1932.

Wieland has set forth in this book his concept of the mechanism of biochemical oxidations and has supported it with evidence drawn from general chemistry and from his own experiments on acetic acid and fermentation and the Schardinger enzyme of milk. The basis of his well known scheme is that oxidation is effected by a transfer of hydrogen from the substance undergoing oxidation, or its hydrate, to a hydrogen acceptor which is thereby reduced, and he has assembled some very interesting sets of data which accord with this hypothesis. An alternative means of accounting for oxidation involves the catalytic activity of iron and about a quarter of the book is devoted to this topic. There is an index and a small bibliography.

Modern Alchemy. *By William Albert Noyes and W. Albert Noyes, Jr. Charles C Thomas, Springfield, Ill.* \$3.00 postpaid. $5\frac{5}{8}$ x $8\frac{7}{8}$; ix + 207; 1932.

"The vicissitudes of the search for transmutation and for healing principles are typical of the progress of science and have been taken as the ground work of this book," say the authors in their preface.

The result is a somewhat superficial survey of a wide variety of subjects ranging from cosmogony to hormones and vitamins. This book must appeal chiefly to the general scientific reader; there are brief and simple explanations of the latest theories of the constitution of matter, the new quantum mechanics, valence, and methods for healing and control of disease. For the benefit of those whose interest is stimulated to further and more profound reading on these subjects there is a list of bibliographical references at the end of each chapter. There is an index.

MEDIZINISCHE KOLLOIDLEHRE. *Lieferungen* 1, 2, 3.

Edited by L. Lichtwitz, Raph. Ed. Liesegang and Karl Spiro. Theodor Steinkopff, Dresden. 5 marks per number. $7\frac{1}{2}$ x $10\frac{1}{4}$; Lief. 1, 80; Lief. 2, 72; Lief. 3, 80; 1932–1933 (paper).

This series when completed will consist of some 10 *Lieferungen*. These first three numbers treat of general theories of colloids with reference to biology and pathology. The following papers are included: Introduction, with sections on protoplasm, aging, assimilation and storage, by R. E. Liesegang; Colloidal-osmotic pressure of biological fluids, by Paul Meyer; Surface tension (capillary electricity and growth), by F. Herčik; Permeability (membranes, theory of adhesive pressure, electric potentials, and thixotropy), by F. Leuthardt; Formation of concretions, by L. Lichtwitz and K. G. Stern; Immunity, by A. Klopstock; and Enzymatic action, by K. G. Stern. Later numbers will discuss the application of colloid research in medicine, and technique.

THE CHEMICAL INVESTIGATION OF PLANTS.

By L. Rosenthaler. Authorised Translation of the Third, Improved and Enlarged German Edition by Sudhamoy Ghosh. G. Bell and Sons, London. 12s. 6d. net. $5\frac{1}{2}$ x $8\frac{1}{2}$; viii + 197; 1930.

This book is intended to provide an introduction not only to the working methods of plant biochemistry but to the logical processes of forming judgments on the suitability of various procedures; which is to say, the subject is treated in somewhat more general terms than in the usual cookbook type of analytical manual. The emphasis is upon quantitative methods throughout. It is meant to be a guide to research in pharmacology and agricultural chemistry, and accordingly there is a useful bibliography of works on special fields. The book opens with a short chapter on the history of the subject—something of a novelty—and closes with a good index.

pH AND ITS PRACTICAL APPLICATION.

By Frank LaMotte, William R. Kenny and Allen B. Reed. The Williams & Wilkins Co., Baltimore. $3.50. 6 x 9; vii + 262; 1932.

This manual is intended for the use of laboratory assistants and technicians in the numerous industrial processes and routine laboratory procedures in which pH measurements find application. The elementary principles of these measurements are explained, and the uses they find in a dozen industries are discussed in separate chapters. A very useful feature of the book is its charts showing typical pH values encountered in practice. There are chapters; on bacteriological and clinical laboratory methods and on soils. There are bibliographies at the end of each chapter and an index.

BIBLIOGRAPHICAL SURVEY OF VITAMINS 1650–1930.

Compiled by Ella M. Salmonsen. With a Section on Patents by Mark H. Wodlinger. Mark H. Wodlinger, 86 East Randolph St., Chicago. $10 net. $6\frac{7}{8}$ x 10; v + 334; 1932.

This excellent bibliography contains approximately 12,000 references in chronological order, covering both foreign and domestic publications, from 1650 to 1930. The bulk of the references occurs after 1916. After that date they are subdivided by type of vitamin. Not only will this bibliography be enormously useful to students working in its particular field, but it also furnishes fine material for statistical

studies of the sort made by F. J. Cole on the literature of comparative anatomy, and E. Wyndham Hulme in broader fields.

Physical Chemistry for Students of Biology and Medicine.

By David I. Hitchcock. Charles C Thomas, Springfield, Ill. $2.75. $5\frac{1}{2} \times 9$; xi + 182; 1932.

The material in this book has been offered during the past five years to medical graduate students in Yale University as a part of the course in physiology. The topics which have been selected from the whole field of physical chemistry are those especially pertinent to biological work, and most essential to an appreciation of modern research. The subject-matter is presented with directness and clarity. There is a bibliography of 96 titles and an index.

Précis de Chimie Physiologique. *Onzième Édition.*

By Maurice Arthus. Revised and brought up to date in collaboration with André Arthus. Masson et Cie, Paris. 65 francs. $4\frac{3}{4} \times 7\frac{1}{2}$; xii + 522 + 5 plates; 1932.

The eleventh edition of a standard work, first published in 1895. Some theories which have proved to be unsound in the light of present day knowledge have been omitted, and considerable new material has been added to bring the book up-to-date.

SEX

Sex and Internal Secretions. *A Survey of Recent Research.*

Edited by Edgar Allen. The Williams & Wilkins Co., Baltimore. $10.00. 6×9; xxii + 951; 1932.

An excellent symposium by twenty-two authorities on the most important recent research in the problems of sex endocrinology, a subject which has had such a rapid growth within the last few years that the research has not been properly evaluated or generally appreciated, and for that reason a survey is greatly to be welcomed.

After a general biological introduction by F. R. Lillie, there are two chapters devoted to a comprehensive discussion of the genetics of sex as found (a) generally in animals, particularly birds and mammals, by C. H. Danforth, and (b) in *Drosophila*, by C. B. Bridges. Embryological foundations of sex in vertebrates are discussed by B. H. Willier, which leads directly to an interesting chapter on sex deviations and the general theories of intersexuality by E. Witschi. The remaining fourteen chapters treat in great detail the physiology of the gonads and the influence of endocrine factors on them as these factors have appeared and been established from laboratory investigations. Riddle contributes an account of the metabolism of sex. The biology of the testes is discussed at length by C. R. Moore, who divides his account into a discussion of testicular activity in the non-mammalian vertebrates and the mammalian, devoting considerable space in the latter section to the factors influencing spermatogenesis. The biochemistry of the testes is summarized by F. C. Koch. The ovarian follicular hormone, theelin, and the biochemistry of this hormone, the physiology of the corpus luteum, and the mammary glands, are discussed with admirable thoroughness in four chapters by E. Allen, E. A. Doisy, F. L. Hisaw, and C. W. Turner. C. G. Hartman gives an interesting account of the recent theories of the mechanism of ovulation, with a description of his own work on the Carnegie monkey colony. Effects of implants of the anterior hypophysis (P. E. Smith) and effects of extracts of the anterior pituitary (E. T. Engle) as well as anterior pituitary changes referable to the reproductive hormones, and the influence of the thyroid and the adrenals on genital function, by A. E. Severinghaus and the two preceding authors, adequately dispose of the pituitary, at present the most popular endocrine gland. There is an important chapter on plumage tests in birds, by L. V. Domm, Mary Juhn and R. G. Gustavson. The last two chapters deal with the subjects of sexual drive (C. P. Stone), and endocrine disorders in sex function in man (J. P. Pratt), which are necessarily treated more generally than the preceding sections owing

to the greater difficulties involved in experimental work along these lines.

Each author reviews critically the work that has been done in the particular subject he is discussing, and points out where the weaknesses lie, and what directions future research may profitably take. Those interested in the progress of sex research will find this book of great value.

THE RHYTHM OF STERILITY AND FERTILITY IN WOMEN. *A Discussion of the Physiological, Practical, and Ethical Aspects of the Discoveries of Drs. K. Ogino (Japan) and H. Knaus (Austria) Regarding the Periods When Conception Is Impossible and When Possible.*

By Leo J. Latz. Latz Foundation, Chicago. $1.00. 4 x 6; vii + 108; 1932.

This book is written in the question and answer method. To quote from the publisher's (and author's) blurb its central thought is: "Women are sterile (cannot conceive) during about three-fourths of the menstrual cycle. The discoveries of Drs. K. Ogino (Japan) and H. Knaus (Austria), which show how the periods of sterility and fertility can be determined, are explained in a popular style." We might add, also in a somewhat sentimental style. By way of illustration we quote questions 14, 55 and 64.

14. What is menstruation?

If the mother cell does not find her 'hero' she languishes and dies within a few hours. She is carried down the Fallopian tube to the uterus, where everything is in readiness to receive a living guest—not a dead mother cell.

The *corpus luteum*, not receiving any information, stops its activities, withers, and decays. The pituitary gland is free to exert its influence. The muscles of the womb again begin to contract and expand, and by so doing expel all the special preparations that were stored up. Blood and mucous substance leave the womb. This phenomenon is called menstruation.

55. What is contraception?

Contraception is the deliberate use of some artificial means (such as voluntary interruption, chemical or mechanical devices), in order to prevent the father cell from meeting the mother cell, in other words, to prevent conception. It means, then, interfering directly with the workings of nature in the marital act.

64. But does periodic abstinence not seem opposed to God's holy will as expressed in the command "Increase and multiply and fill the earth" (Gen. 1, 28)?

If the literal meaning of these words is stressed too much, every person reaching puberty would have to enter the married state, vows of chastity would have to be abrogated, married people would not be allowed to observe continence and would be obliged to bring into the world a maximum number of children. This evidently cannot be the meaning of the text, nor can it be the will of God.

Our Catholic friends are apparently leaning more heavily upon this treatise in their anti-birth control propaganda than its merits warrant. There may be a dependable "safe period" in the reproductive cycle of the human female, but if there is that fact will be established by physiological rather than biblical research, we opine.

THE PRACTICE OF BIRTH CONTROL. *An Analysis of the Birth-Control Experiences of Nine Hundred Women.*

By Enid Charles. Williams and Norgate, London. 10s. 6d. net. $5\frac{1}{2}$ x $8\frac{1}{2}$; 190; 1932.

This book is devoted to the analysis and discussion of data regarding the prevalence and effectiveness of contraceptive methods as used in England. The material used is derived from three sources. The first is from questionnaires sent out by the Birth Control Investigation Committee of England; the second from questionnaires collected by Nurse Daniels from persons who had been supplied and fitted by her with Dutch caps; the third from the records of the Birmingham Women's Welfare Center (a birth control clinic). From the first source 432 cases were available for analysis; from the second, 198; from the third, 244. Out of the total number of women in the three series (874) there were exactly 12 (p. 23) who had never used any contraceptive method whatever, available for comparison with women who had used some method or other. This is admittedly an inadequate control. The author is, therefore, of necessity, thrown back upon making comparisons between different contraceptives.

A great variety of other questions are, however, discussed statistically and otherwise in the volume. Indeed the diffuseness of the treatment, and a readiness to base discussions of very broad and complex problems of fertility upon material that fails to satisfy some of the simplest canons

of sound scientific methodology, leaves an unfortunate impression regarding an obviously sincere, honest, and laborious undertaking. The book will, however, be useful for purposes of comparison to other students in the same field, within its limitations. It is refreshingly free from propaganda. And in so difficult and complicated a field as that of human reproduction in its relation to population problems any contribution, however modest, is welcome.

THE SEX TECHNIQUE IN MARRIAGE.
By Isabel E. Hutton. Emerson Books, New York. $2.00. 5 x $7\frac{1}{2}$; 160; 1932.

THE HYGIENE OF MARRIAGE. *A Detailed Consideration of Sex and Marriage.*
By Millard S. Everett. The Vanguard Press, New York. $2.50. $5\frac{1}{2}$ x 8; 248; 1932.

The first book, with its four pages of laudatory press opinions, will no doubt continue to find favor among those persons, both medical and lay, who believe that a superficial knowledge of the anatomy and physiology of sex, mixed with pious admonitions, will help to solve the difficult problems of sex in marriage.

Professor Everett, although not himself medically trained, has written a more comprehensive, a less dogmatic, and withal a better book. The last four chapters under the headings: the need for birth control, birth control laws, birth control clinics, and scientific versus hearsay methods of contraception, are particularly well done and give the information desired by most people who seek out and read such books.

PARENTS AND SEX EDUCATION. *For Parents of Young Children.*
By B. C. Gruenberg. Viking Press, New York. $1.00. $5\frac{1}{8}$ x $7\frac{5}{8}$; viii + 112; 1932.

The problem, which all parents face, of how and what to teach their children about sex, is approached in this book from a thoroughly realistic point of view. The author recommends as a first step the adoption of a matter-of-fact point of view toward the whole question of sex by the parent. Suggestions based on sound child psychology and characterized by definiteness are then outlined for meeting the situations most commonly arising, and for forestalling undesirable situations. The final chapter presents supplementary biological information for parents. The treatment throughout is practical and unsentimental.

BIRTH CONTROL.
By Johann Ferch. Translated with a Biographical Foreword by Christian Roland. Edited, with an Introduction, by A. Maude Royden. 3s. 6d. *Rider and Co., London.* $4\frac{3}{4}$ x $7\frac{5}{8}$; 124; 1932.

In this book the founder of the Austrian League for the Protection of Mothers discusses the ethics of birth control and the methods of contraception used by the League. No method, he admits, is able to prevent impregnation with absolute certainty. As an interim measure until the knowledge of birth control is more widely disseminated and more certain methods are discovered he also advocates the legalization of abortion during the first three months. On the latter point Maude Royden and the translator do not agree with him.

MAN AND WOMAN IN MARRIAGE.
By C. B. S. Evans. Bruce-Roberts, Chicago. $2.00. $4\frac{3}{4}$ x $7\frac{1}{8}$; 113; 1932.

This little book is one of the clearest and most sensible expositions of the *ars amandi* that we have seen in some time. The importance of the wife's reaching an orgasm and the technique of insuring that result are emphasized. There is no bibliography or index.

BIOMETRY

STATISTICAL METHODS FOR RESEARCH WORKERS. *Fourth Edition—Revised and Enlarged.*
By R. A. Fisher. Oliver and Boyd, Edinburgh and London; G. E. Stechert and Co., New York. 15 shillings net (Great Bri-

tain); $4.00 (U. S. A.). $5\frac{1}{4}$ x $8\frac{3}{4}$; xiii + 307 + 7 folding sheets of tables; 1932.

That this book has reached a fourth edition in seven years speaks well for its usefulness. The principal additions to this edition deal with the analysis of covariance. The appendix to the chapter on frequency distributions has been rewritten to include the *k*-statistics and cumulants, "since the inconveniences of the moment notation seem now definitely to outweigh the advantages formerly conferred by its familiarity." There are a bibliography and an index.

As to the Method of Maximum Likelihood, which forms the corner-stone of Fisher's statistical philosophy, we are still uncertain whether it is more than a verbal evasion of the difficulties of inverse probability. However, the only alternative to some such method seems to be inductive agnosticism; we are, therefore, disposed to accept it in practice, while entering a caveat as to its theoretical foundation.

Elementary Mathematics from an Advanced Standpoint. *Arithmetic. Algebra. Analysis.*

By Felix Klein. Translated from the Third German Edition by E. R. Hedrick and C. A. Noble. The Macmillan Co., New York. $3.00. $6\frac{1}{8}$ x $9\frac{1}{4}$; ix + 274; 1932.

Besides his important mathematical researches Klein was interested in the teaching of mathematics, not only in the universities, but in the secondary schools. The lectures which he gave for many years to secondary school teachers of mathematics were finally printed, and the present volume is a translation of Part I of this work. Among the points which Klein emphasizes in the teaching of mathematics are the importance of the function concept, the mutual connection between problems in various fields, the necessity in elementary and secondary instruction of a concrete and intuitional approach to mathematical concepts, and the value of a historical treatment of the development of mathematics. There are numerous bibliographical references in the text and an index.

PSYCHOLOGY AND BEHAVIOR

Development of an Infant Chimpanzee during her First Year. *Comparative Psychology Monographs Vol. 9, No. 1, Serial No. 41.*

By Carlyle F. and Marion M. Jacobsen and Joseph G. Yoshioka. Johns Hopkins Press, Baltimore. $1.50. $6\frac{7}{8}$ x 10; 94; 1932 (paper).

In this paper Carlyle and Marion Jacobsen contribute the introduction and the section on behavioral development, and Joseph G. Yoshioka the section on physical growth and physiological maturation. There is a foreword by Robert M. Yerkes. The parents of this baby chimpanzee (Alpha, born 246 days after conception) were well known as to their psychobiological characteristics, having been under close observation for several years previous to the birth of their offspring. They had only just come into sexual maturity. Since the mother refused to care for the baby the investigators were able to rear her in isolation from her kind for many months and to obtain a unique and important series of observations covering many phases of her growth and development. Comparing the chimpanzee records for the first seven months with records of human infants for an equal period the graph shows that

> In creeping, sitting and walking the chimpanzee infant is increasingly accelerated over healthy human infants; that the chimpanzee is also accelerated in skeletal development, the arms more so than the legs; and that the extent of the behavioral acceleration approximates closely that of the skeletal.

Concerning the relatively simple tests of eye-hand coördination Alpha was equal to or slightly accelerated over the human child. In imitation Alpha failed completely in the first year, and succeeded in passing only the simplest items in the second year. Comparing Alpha's behavior tests with those of the human infant, the investigators note the following points:

> Although the chimpanzee passed many test items at the lower age levels, toward the end of the year she had reached a point beyond which she made but little progress. The absence of language did not appear to be the immediate cause of such failure since

numerous non-language tests involving imitation and exploitive behavior were failed. Examination of Alpha in the second year, and incidental observations on older chimpanzees, have indicated that within marked limits the chimpanzee is capable of performing additional test items but only after greater experience and development. Among the test items which were passed, the temporal sequence in which they were accomplished followed rather closely the order for the human infant.

In the majority of test situations other than postural and locomotor development the chimpanzee tended to maintain about the same age level as the average human child. The volume includes tables and charts exhibiting growth rates, etc.; an appendix in which is given the responses to Gesell normative items; a brief bibliography; an index and a series of plates showing Alpha in infancy.

REMEMBERING. *A Study in Experimental and Social Psychology.*

By F. C. Bartlett. The Macmillan Co., New York. $5.00. $6\frac{1}{8} \times 9\frac{1}{2}$; x + 317; 1932.

A book for the student and experimentalist rather than for the general reader. The work had its origin in an investigation to determine the different factors (and their functions) involved in the course of normal visual perception. It was necessary to extend the study to related mental processes and in particular to a study of imagery and recall. While the work was mainly in individual perceiving, imagery and remembering, it included also experiments with social groups as units. The investigator adopted a strictly functional point of view:

> All considerations of the descriptive characteristics of *what* is perceived, imaged or remembered have been kept in a secondary position. The central problems all the time have been concerned with the *conditions*, and the variety of conditions, under which perceiving, imaging and remembering take place.

The first 227 pages of the book present the experimental work. "Remembering," the author states in the chapter devoted to his theory, "is not re-excitation of innumerable fixed, lifeless and fragmentary traces."

> It is an imaginative reconstruction, or construction, built out of the relation of our attitude towards a whole active mass of organised past reactions or experience, and to a little outstanding detail which commonly appears in image or in language form. It is thus hardly ever really exact, even in the most rudimentary cases of rote recapitulation, and it is not at all important that it should be so. The attitude is literally an effect of the organism's capacity to turn round upon its own 'schemata,' and is directly a function of consciousness.

The latter part of the book is concerned with the study of specific social influences upon remembering such as social psychology, social psychology and the matter and the manner of recall, conventionalisation, the notion of a collective unconscious, and the basis of social recall. While the author occasionally refers the reader to the work of other investigators, he includes no literature list. The work contains a few figures and plates and is indexed.

THE PHYSICAL MECHANISM OF THE HUMAN MIND.

By A. C. Douglas. The Williams & Wilkins Co., Baltimore. $4.00. $5\frac{3}{8} \times 8\frac{1}{2}$; xiv + 251; 1932.

The problems of presenting a theory of mind in such a way that both the intelligent general reader and the specialist in psychology will be interested presents numerous difficulties. That is what the author of this book has attempted to do. That he has succeeded in his project those readers who belong in the first class will agree. The specialist will no doubt find flaws, but even so will admit that the book merits his attention. More than one sitting will be required by the layman to master the book. In spite of the clear and logical manner of presentation the substance is far too meaty to be digested rapidly. In the preface the author briefly outlines the two main currents of thought which lead up to *Associationism* and the recent trend towards *Behaviorism* in America and *Gestaltism* in Germany. Then he states the aim of the present work:

> I believe, and I hope to demonstrate, that by taking full advantage of the latest advances in physiological knowledge the gaps left by Associationism may be filled, the criticisms and requirements of Gestaltism may be met, and a complete scientific theory of Mind may be presented, upon the materialistic basis which Behaviourism rightly demands.

Up to Chapter X such subjects are discussed as the principles of nerve arrangement and nerve action in the higher vertebrates and man, the elements of psychoneural correlation, the mechanism of space-time perception and habit, instinct and motion. It is clearly brought out that the phases of mind so interlock and interpenetrate that in order to understand one the whole field must be arrayed. The latter part of the book (pages 144 to 244) is concerned with the construction of his theory. The work includes figures and diagrams, a bibliography of 33 titles, a brief list of books on psychology for the general reader, and an index.

THE USE OF THE SELF. *Its Conscious Direction in Relation to Diagnosis, Functioning and the Control of Reaction.*
By F. Matthias Alexander. E. P. Dutton and Co., New York. \$2.00. $5\frac{1}{8} \times 7\frac{1}{2}$; xix + 143; 1932.

Doctor Dewey in an introduction enthusiastically endorses Mr. Alexander's methods of central and conscious control. He says:

> If there can be developed a technique which will enable individuals really to secure the right use of themselves, then the factor upon which depends the final use of all other forms of energy will be brought under control. Mr. Alexander has evolved this technique.

In the first part of the book the author describes in detail his experiment by means of which he was able to correct faulty habits in speaking and reciting. He discovered that

> my sensory appreciation (feeling) of the use of my mechanisms was so untrustworthy that it led me to react by means of a use of myself which *felt* right, but was, in fact, too often wrong for my purpose.

Lengthy experience as a teacher verified this belief in the prevalance of sensory untrustworthiness and its significance in the problem of the control of human reaction. Separate chapters deal with the problems of the stutterer and of the golfer who cannot keep his eye on the ball. In the final section on diagnosis and medical training emphasis is placed on the importance to the physician of a training in the satisfactory direction of the use of his own mechanism. This would enable him

> to judge the manner of use present in the patient, detect any misdirection of use, and, when this exists, determine its relation to any symptoms of unsatisfactory functioning present.

The book is indexed.

HABITS. *Their Making and Unmaking.*
By Knight Dunlap. Liveright, New York. \$3.00. $5\frac{3}{4} \times 8\frac{5}{8}$; x + 326; 1932.

The purpose of this volume is "to outline the interrelation of the processes of learning and unlearning, of habit making and habit breaking," and in an elementary way "to show how a fuller understanding of the learning process makes possible more adequate procedure in the breaking of disadvantageous habits."

Dunlap in his discussion of the psychology of learning has abandoned the conventional method to be found in so many text books for a position which in many instances seems almost revolutionary. He by no means claims that his interpretations are final. That he has succeeding in casting aside many of the false premises which have so long befogged psychological studies and established a sounder, more rational basis for future work his book amply testifies. The headings of the 12 chapters are as follows: The problems of habit and learning; The fundamental principles of learning; Voluntary and involuntary action; Physiological theories of learning; The process in learning; The conditions of efficient learning; Retaining, recalling and relearning; Remembering and forgetting; Personal and social adjustment; The breaking of specific bad habits; Habits of emotional response; Learning ability and intelligence. The work is not too formidable for the lay reader although the last four chapters dealing with practical application will undoubtedly receive his closest attention. There is a bibliography and an index.

A STUDY OF ERROR. *A Summary and Evaluation of Methods Used in Six Years of Study of the Scholastic Aptitude Test of the College Entrance Examination Board.*

By Carl C. Brigham. College Entrance Examination Board, New York. $5.00. $8\frac{1}{2}$ x 11; xiii + 384; 1932.

The first two chapters of this book are theoretical. Chapter I consists almost entirely of excerpts from the writings of Titchener and Dewey whose antithetical points of view, the one psychological, the other societal, are contrasted. Spearman is found to occupy both positions. The use of symbols as a means of communication between individuals is discussed in Chapter II. The author offers the following definition of the science of education:

> that science which regards experience as dependent upon a pluralism of communicating individuals. The subject-matter of this science, formally considered, is societal, and, materially considered, is symbolic.

In analyzing the results of the Scholastic Aptitude Tests the methods of correlation and partial correlation are used. The tests themselves fall into five groupings: synonyms, analogies, antonyms, double definitions and paragraph reading. The intercorrelations between these tests are very high.

The remainder of the book is devoted to methods of treating symbols objectively. Chapter III presents an experiment in using pictorial instead of verbal material in the test composition. In the following chapters the various tests are studied intensively for significance and reliability. It is interesting to note that each type of test material showed approximately identical solutions when repeated on a population similarly sampled. Separate chapters are devoted to evaluations of the arithmetic tests and the spatial relations tests. The appendices include a description of the administration of the tests, and the six annual reports (1926–1931) of the College Entrance Examination Board.

STUDIES IN CONCEPT FORMATION. *I. The Development of the Concept of Triangularity by the White Rat. Comparative Psychology Monographs, Vol. 9, No. 2, Serial No. 42.*

By Paul E. Fields. The Johns Hopkins Press, Baltimore. $1.25. $6\frac{5}{8}$ x 10; 70; 1932 (paper).

This volume presents evidence to support the theory that each individual (infrahuman included) has evolved his own concepts and that there must be a period during which the concept is developed, in contradistinction to the theory that concepts are peculiar to man and are present in him ready-made. Specifically, the purpose of this paper is to determine, granted that a white rat is able to discriminate an equilateral triangle (apex up) from a circle of equal area and brightness, whether this discrimination is based upon the rat's recognition of the qualities of triangularity as opposed to the qualities of circularity, or whether the discrimination merely results from the reaction of the rat to a differential retinal distribution of light without any reference to the qualities inherent in such distributions. Eleven white rats were given a total of over 40,000 trials to 80 different stimulus cards which were presented in more than 240 combinations. The conclusion drawn from the data which were obtained is that

> when white rats are given a training period specifically designed to provide a large number of different "triangle experiences," the rats are able to perfect a type of behavior which is fully described by the implications inherent in our use of the term "concept."

THE MEDICAL VALUE OF PSYCHOANALYSIS.

By Franz Alexander. W. W. Norton and Co., New York. $2.75. $5\frac{1}{4}$ x 8; 247; 1932.

This book is a simple, straightforward account of the psychoanalytic doctrine. The subject-matter is treated as a science and not as a dogma, an accomplishment which is the more commendable because it is so rare. The significance of psychoanalysis for medicine is seen in the following two accomplishments:

> 1. With the help of a technique specifically adapted to the nature of psychic phenomena, it has developed a consistent and empirically founded theory of the personality, fit to serve as a basis for the understanding and treatment of mental disturbances. 2. It has given a concrete content to the philosophic postulate that living beings are psychobiological entities, by investigating in detail the interrelation of physiological and psychological processes. The greater part of these investigations must, however, be left to the future for completion.

The second chapter, in which the author describes the present status of psychoanaly-

sis as a theory and as a therapeutical system, is especially interesting. The intimate relation of the therapeutic concepts to the general theory is emphasized. The contents of this chapter are restricted to the concepts which are most essential and empirically best founded.

In chapter III the psychoanalytic treatment of psychoses is critically considered. Chapter IV is devoted to a discussion of psychogenic factors in organic diseases, and the final chapter considers the place of psychoanalysis in medical education. The book is well indexed.

SCHLAF UND TRAUM.

By Hans Winterstein. Julius Springer, Berlin. 4.80 marks. $4\frac{5}{8} \times 7\frac{1}{4}$; 135; 1932.

DIE WELT DER SINNE. *Eine gemeinverständliche Einführung in die Sinnesphysiologie.*

By W. v. Buddenbrock. Julius Springer, Berlin. 4.80 marks. $4\frac{5}{8} \times 7\frac{1}{4}$; vi + 182; 1932.

These two books form Volumes 18 and 19, respectively, of the *Verständliche Wissenschaft* series, a series of scientific treatises planned with the general reader in mind. Several numbers have already been noticed in this REVIEW.

The first of the two noticed here is a very readable exposition of the physiological, pathological and psychological aspects of sleep and dreams. The section on the Freudian theory of dreams seems to us fair enough, though Winterstein does not swallow it whole.

Buddenbrock describes in an interesting manner the five senses, broadly speaking, plus the senses of temperature, gravity, and proprioceptive stimulations, their presence, or absence, the various mechanisms involved and their mode of functioning in various organisms from microscopic animals to man. It would make an excellent text for supplementary reading in a scientific German course.

Both of these books are illustrated and the first is furnished with an index.

MOTIVATION OF YOUNG CHILDREN. *An Experimental Study of the Influence of Certain Types of External Incentives Upon the Performance of a Task. University of Iowa Studies. Studies in Child Welfare, Volume V, Number 3.*

By Lucile Chase. University of Iowa, Iowa City. \$1.00 (paper); \$1.35 (cloth). 6 x $9\frac{1}{4}$; 119; 1932.

This volume presents an experimental investigation of the influence of external incentives upon the performance of tasks done by young children. The study was made on 213 children ranging from two to eight years in age. They were divided into four groups, one serving as a control. In testing the children the motivation-dynamometer, an apparatus devised by the author, was used. The relative effectiveness of repeating directions only between trials, of giving praise between trials, and of giving rewards is determined by comparing the test scores of the groups. The scores were lowest in the first case and highest in the last. The children were tested again, this time for the relative effectiveness of repeating directions only between trials, giving reproof, and giving punishment. The scores in the last two cases show no significant difference, but the differences between the scores of each of the last two cases and the first approach significance. In all of the tests, the control group, receiving only control-motivation, scored lower than the experimental groups receiving any one of the three types of incentive. A bibliography of 57 titles is given.

LYING AND ITS DETECTION. *A Study of Deception and Deception Tests.*

By John A. Larson, in collaboration with George W. Haney and Leonarde Keller. University of Chicago Press, Chicago. \$5.00. 6 x 9; xxii + 453; [1932].

The book has much of the fascination that a good detective story has, besides containing an accumulation of carefully criticized literature on the subject. Each type of deception is described and classified; ancient and modern methods used by the police and other officers to deal with criminals are reviewed and shown

to be weak and inadequate. The physical and emotional disturbances concomitant with lying are discussed at length, and there is an interesting section on modern scientific technique in handling criminals. The most valuable part of the book is the final section in which the author gives an outline of his own researches in developing a test instrument (cardio-pneumo-psychograph) to detect emotional responses in individuals. While not perfect this method when combined with others will undoubtedly give valuable additional means for detecting a criminal.

DESIRE AND CREATION.

By K. W. Monsarrat. Henry Young and Sons, Liverpool. 5 shillings net (postage 5 pence). $5\frac{3}{8}$ x $8\frac{1}{2}$; 104; 1932.

The author cannot reconcile the trend towards progress with the concept of natural selection and random variation in the individual. He therefore produces a new theory, which is

> that if a living organism corresponds with the unfamiliar and this correspondence is followed by adaptation, a change that has permanence may arise from its own act and may be transmitted to a succeeding generation.

Also, he states that the animate is distinguished from the inanimate, in that it can direct its energy towards work and ultimately creation. Whatever case the author may be trying to make is considerably weakened in the last three chapters, where he writes with a certain lyrical mysticism about the "desire to give" as the greatest thing in life. There is neither index nor bibliography.

CHILD PSYCHOLOGY.

By Buford J. Johnson. Charles C Thomas, Springfield, Ill. $4.00. 6 x 9; xii + 439; 1932.

There is a great deal in this book that is excellent. The subject-matter both covers the literature and presents new studies made in the Child Institute of the Johns Hopkins University. As indicated by the chapter headings, among the points analyzed are the following: infant responses, locomotion, manipulation, speech, thought, emotion, social behavior and personality, and individual differences. No especially new conclusions emerge and no new hypothesis is presented. The book is primarily didactic. It is unfortunate that the use of complex verbiage often obscures the real meaning of a sentence, a criticism which applies to many academic psychologists' presentation of otherwise excellent material. The book contains a bibliography of 206 titles. There are author and subject indices.

MAN AS PSYCHOLOGY SEES HIM.

By Edward S. Robinson. The Macmillan Co., New York. $2.50. $5\frac{1}{2}$ x $7\frac{3}{4}$; 376; 1932.

For the layman who is more familiar with the lingo than with the actual content of present-day psychological theory and points of view, this book provides an excellent medium for orientation. The subject-matter is presented in two parts. The first part, *Man, comments on his nature*, discusses motivation, the heredity vs. environment controversy, the mechanism of the learning process, man as a functioning personality, and the mind-body controversy. The point of view is detached and practical. The presentation is clear and humorous. Part II, *Psychology, its aims, its deeds, its follies*, is especially interesting in its swift, unbiased survey of psychological methodology, precepts and trends. There is a bibliography and an index.

THE STORY OF SCIENTIFIC PSYCHOLOGY.

By Adelbert Ford. Sears Publishing Co., New York. $3.00. $5\frac{1}{2}$ x $8\frac{1}{2}$; xii + 307; 1932.

The general reader and especially those who struggled through the maze of Psychology I in the late Victorian Era, will find this an interesting and informing book. Professor Ford, of Lehigh University, has done *Scientific Psychology* somewhat in the manner of Paul deKruif's *Microbe Hunters*. In his preface he says:

I have written this book to present something of the dramatic history of the science of psychology, showing the peculiar part played by the personalities of research men, the sacrifices made to achieve pure scientific truth, and the nature of some of the findings made in the process of attaining predictability in a subject which was for years in the hands of the mystics.

AN EXPERIMENTAL STUDY OF SUPERSTITIONS AND OTHER UNFOUNDED BELIEFS *as Related to Certain Units of General Science.*

By Otis W. Caldwell and Gerhard E. Lundeen. Bureau of Publications, Teachers College, Columbia University, New York. $1.25. 6 x 9; 138; 1932 (paper).

When discussions of commonly accepted unfounded beliefs, such as that red hair is a sign of violent temper or that lightning never strikes twice in the same place, were incorporated in high school general science class work, a larger proportion of the pupils gave conventionally correct responses in a test than had done so before the discussion. The authors admit that

It would be more desirable to measure changes in attitudes by a study of reactions individuals make when faced with life situations which may influence behavior by belief in unfounded ideas. An adequate technique for measuring attitudes in this way has not been devised.

LES TROUBLES DU SOMMEIL. *Hypersomnies, Insomnies, Parasomnies.*

By Henri Roger. Masson et Cie, Paris. 20 francs. $5\frac{1}{2}$ x $7\frac{3}{4}$; 206; 1932 (paper).

A detailed study of insomnias, hypersomnias, and parasomnias and their causes, together with a critical discussion of therapeutic treatments used in overcoming them. There is a subject index but no bibliography.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE PHILOSOPHY OF PHYSICAL REALISM.

By Roy W. Sellars. The Macmillan Co., New York. $4.00. $5\frac{3}{4}$ x $8\frac{5}{8}$; xiv + 487; 1932.

In this book the author of *Critical Realism* develops his philosophy further. According to this the mind is not imprisoned within its own walls, as Berkeley and his followers had taught, nor, on the other hand, does it literally reach out and touch the stars, as the neo-realists contended. Through meanings founded on sense data the mind gains approximate knowledge of external things. "It is the pattern of things that we can decipher, even though we cannot apprehend the stuff of being."

He rejects the belief in universals "as a peculiar kind of entity in external things which may be in many things at once and gives them an identity of nature." The members of a class are not identical but similar in some respect, and on the basis of this similarity the mind thinks them in terms of the same predicate. It is a matter of logical, not of ontological, identity.

Space, as the extendedness of physical systems, and time, as change or eventness, are accepted by the author. The theory of relativity, he concludes, is a theory of measurement and of the operational interpretation of numbers attached to magnitudes and does not have the ontological significance sometimes ascribed to it.

And I am conservative enough to defend the category of substance against both idealist and eventist. Yet I do not defend a Lockian parody of it. It stands for primary and secondary continuants which are spatial and the *locus* of events and which appear in scientific *description* as space-time worms. There is no inert core to which entities called properties are attached. It is the concrete continuant which we know in terms of what is disclosable about it, which we call its characteristics and executive properties.

As to causality he rejects Russell's attempt to reduce it to regular sequence or uniformity.

Consciousness is for him a quality of brain-events and therefore "as spatial as the brain of which they are events." Finally, valuing is as objective in reference as knowing, but judges an object with respect to human living.

The lover of ingenious paradoxes will, no doubt, find this book pedestrian. To this the author would probably retort that the lover of paradoxes is not the best judge of a system of philosophy.

THE NATURAL SCIENCES. *An Introduction to the Scientific Philosophy of To-day.*

By Bernhard Bavink. Translated from the Fourth German Edition with Additional Notes and Bibliography for English Readers, by H. Stafford Hatfield. The Century Co., New York. $7.50. 6 x 9; xiii + 683; 1932.

Bavink is more concerned about the processes by which one arrives at scientific knowledge than he is about specific results. He appears at his best in the first half of the book, which is devoted to physics and cosmology, fields in which he is most at home. He expounds the newer concepts of these subjects with a clearness and a plausibility that is often absent from such discussions. The other half, titled "Matter and Life" and "Nature and Man," is material more familiar to biologists; these sections should be most useful to interested laymen. Bavink's biology is mostly *Entwicklungsmechanik*, genetics, and evolution, and he deals with its problems as philosophers are wont to do. Mechanism and vitalism, determinism and teleology, the problem of consciousness, and the inheritance of acquired characteristics are all given an airing. In matters of science and religion he takes a conciliatory position. In fact, one of the curious features of the book is the utter earnestness with which he considers such topics as astrology, telepathy, and spiritualism; while he comes to the same conclusions that most scientific men reach he apparently found it harder to convince himself than is usual.

SCIENCE AND SUPERSTITION IN THE EIGHTEENTH CENTURY. *A Study of the Treatment of Science in Two Encyclopedias of 1725–1750. Chambers' Cyclopedia: London (1728). Zedler's Universal Lexicon: Leipzig (1732–1750).*

By Philip Shorr. Columbia University Press, New York. $1.50. $5\frac{7}{8}$ x $8\frac{3}{4}$; 82; 1932.

In that system of conventional generalizations which passes for history with most of us the eighteenth century is labeled an Era of Enlightenment, in which superstition had given way to science. But in the human mind mutually contradictory ideas can live together more or less peacefully. There is no sharp break between cultural periods: old superstitions can continue to exist side by side with new sciences. Some years ago Lynn Thorndike showed that in Diderot's famous *Encyclopédie* there were abundant remains of earlier superstitions. In this interesting book the author extends the analysis to two other eighteenth century encyclopedias and finds in them a still greater survival of unfounded beliefs. Thus in Chambers' *Cyclopedia* "The great objectives of alchemy are enumerated without a shadow of scepticism" and Galen's remedy for hydrophobia, "to feed the patient a spoonful of ashes of either crawfish or river lobsters twice a day for forty days," is given as an infallible cure. In short, the eighteenth century was still much more an age of transition than we are accustomed to realize.

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THE QUARTERLY REVIEW *of* BIOLOGY

MORPHOGENESIS OF THE SHOULDER ARCHITECTURE PART I. GENERAL CONSIDERATIONS

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INTRODUCTION

THE problem of limb development has received, during the past hundred years, the critical attention of a host of able morphologists, but as the sum of knowledge increases new light can be shed on the problem from time to time. One of the chief difficulties encountered in any such morphological investigation lies in the fact that even the lowest of our living vertebrates are probably as old phylogenetically as our highest and have had time to evolve many complicated and often misleading details of a tangential character, which may prove exceedingly difficult to evaluate.

In any study of the appendages equal regard must be accorded neurological, myological and skeletal features. No one of these can be discussed without a consideration of the others, from all possible angles that may apply, paying due regard to the alterations which these systems probably can or can not experience. Consideration must also be given to the evolution of posture, of locomotion, and to changes in environment. This the author attempts to do for the extrinsic and intrinsic structures of the pectoral girdle. He, of course, entertains no delusions that he can settle all of the points at issue, for many of them will remain controversial forever.

The basic facts concerning the pectoral appendage can be understood only by a scrutiny of all facts that may have a bearing on the subject, from the lowest to the highest forms. Hence the present report will be divided into a preliminary or general section, another on fish, and subsequent chapters on the higher vertebrates.

EMBRYOLOGY

No proper discussion of nerve, muscle and bone can be undertaken without a brief exposition of their most salient embryonic features.

The neurological details most pertinent to the present study are phylogenetic rather than ontogenetic, and this system needs scant attention from the embryonic viewpoint. The nervous system is entirely derived from the neural plate of the ectoderm. That originally it was seg-

mental in character has frequently been claimed, but the more conservative school of thought holds that such suggestion of neuromerism as occurs is secondarily effected to conform to the metamerism of the somites, and recent experiments tend to uphold this viewpoint. The important feature is that invariably there is a pair of motor and a pair of sensory nerves given off by the spinal cord to each segment and that the motor root invariably innervates the myomere of the same segment. It was long considered that the early differentiation of the muscular system was actually influenced by the nervous system, but the myotome is laid down before the nerve reaches it. In fact the actual connection between nerve and muscle, by the motor end plates, is not effected until a stage at which practically all the muscle divisions have become differentiated (Cajal, 1928), and muscles would doubtless continue to develop to a postnatal stage even if their nerves could be completely extirpated.

The reason why a nerve filament always reaches the particular muscle for which it is destined is a matter that has received much controversial attention. It may be no more remarkable than the astonishing way in which some of the peripheral structures are laid down in an unvarying pattern, but the situation is different, for nerves, unlike most other anatomical details, actually grow by pushing out from a central area. They follow prescribed and often circuitous pathways with but relatively slight deviation from the normal. The subject is too much involved to discuss or even summarize here, but it is the opinion of Cajal, one of the greatest authorities on the question, that there is a definite neurotropic influence concerned: that specific stimuli for the orientation of the nervous cones of growth are particularly numerous in the embryonic period, the most active then appearing to be elaborated by the myotome, connective tissue, and neurones that are forming dendrites.

The fact that interests us here is that the proper nerve practically invariably reaches its proper muscle, but if this be prevented experimentally, then apparently there will be an effort made for innervation of the muscle by other nerves. It is not improbable that the latter can occur on rare occasions as an abnormality, and an appearance of heterotopic innervation be given.

Bone is classified as of two sorts, enchondral and intermembranous, but the basic difference may not be as great as is often implied, and a few osseous elements (sphenoid and temporal) are derived from both. Intermembranous bone was apparently first formed from mesenchyme at the base of such dermal elements as placoid scales and became extensive where originally there was need for surface strengthening, through the secretion of ossein and lime salts.

Enchondral bone can be divided into two categories, comprising structures derived essentially from mesoderm, and those with an origin largely ectodermal. The first of these groups may again be subdivided for convenience into those skeletal elements contributing to the chondrocranium, which, whatever may have been their original purpose, serve for the protection of vital parts, and those which have formed as the result usually of muscular stress. In the latter case the situation is almost invariably in intermuscular septa (exception, sesamoid bones), and the development is by condensation of (theoretically) any part of the mesenchyme. The second enchondral group, comprising the branchial cartilages, including Meckel's cartilage, palato-quadrate, etc., was found by Landacre (1921) to be derived, at least in urodeles, from ectoderm by differentiation of neural crest elements, and Stone (1926)

has recorded the formation of cartilage in transplanted neural crest. The exact significance of this is not yet understood.

Cartilaginous bone is formed in the lower vertebrates mostly by perichondral ossification invading cartilage, while in the higher forms enchondral ossification is the rule. In the cartilaginous fishes local calcification of cartilage frequently occurs.

All muscular tissue, except the intrinsic muscles of the eye ball and of the smooth skin musculature (of the skin glands), is usually conceded to be derived from embryonic mesoderm, although there appears to be some question concerning the precise derivation of the branchial components. In regard to the somatic musculature at least there is first formed dorsally, along both sides of the notochord, a pair of myotomes to each somite. These are sac-like, enclosing a myocoelic cavity which soon disappears. From them are derived all those back muscles originally situated dorsal to the lateral line organs, as well as cutis and osseous elements.

A frequent misconception regarding the development of the musculature is to the effect that the muscles ventral to the lateral line are formed by actual growth in that direction of the original, dorsally-situated myotomes. Conditions vary in different parts of the body, but in the anterior trunk at least there appears to be a lateroventral muscle mass entirely distinct from the dorsal myotome. Between the two there is a connective tissue septum, and tending further to separate them at early stages of phylogeny are the pronephros and its duct, and the lateral line structures. The lateroventral musculature differentiates by condensations of mesoderm progressively in a ventral direction, forming a lateral somatopleure, giving rise to the somatic musculature, and a medial splanchnopleure, from which is derived the smooth musculature of the intestinal tract. Whether or not all the striated branchial muscles are also derived from this element is not entirely certain. Between the two plates is a coelomic cavity. In other parts of the body, or in vertebrates that have long since discarded all vestige of a lateral line system the distinctiveness in origin of the dorsal from the lateroventral musculature tends to become obscured in the embryonic picture.

Joining the somites are myosepta, but the segmental character of most of the musculature has been lost in the higher vertebrates.

The initiation and early growth of muscles appear to be independent of the nerve supply, just as the eye will continue to grow for a time when transplanted to another part of the body.

In the fish it has been demonstrated that the musculature of the appendages is formed by budding of the myomeres, as explained later, and the character of the innervation suggests that in all vertebrates the limb muscles had similar derivation. In the higher forms, however, the initiation is by condensation directly from the mesoderm of the limb buds themselves. It may not be illogical to assume that in these the early budding stage has dropped out of the embryological picture; otherwise the doctrine of the continuity of vertebrate phylogeny becomes doubtful.

GENERAL CONSIDERATIONS OF THE NERVOUS SYSTEM

The nervous system has played a far more forceful rôle in the phylogeny of vertebrates than is generally conceded, and certain of its characteristics must here be discussed.

Branchiomeric nerves. Although embryology appears to indicate that the central nervous system has not had a segmental or

neuromeric origin, a form somewhat simulating segmentation has been at least secondarily assumed, to conform to the myomeres. In the case of the cranial nerves this is more graphically illustrated by such protovertebrate forms as ostracoderms. In these Stensiö (1927) shows what clearly appears to have been an oral (or vestibular) branch and a second pharyngeal branch of n. trigeminus (V) succeeded by components of nn. facialis (VII), glossopharyngeus (IX), and vagus (X), all to successive branchiosepta (fig. 1). Other branches of the vagus supplied a more posterior series, successively smaller, of branchiosepta. There is every reason for assuming that this was essentially the basic plan, that the vagus nerve originally supplied one or two of the posterior gill segments, and that additional segments, with vagus innervation, were added to the end of the series as the need arose.

Occipitospinal nerves. It is now well known that in at least some of the members near the bottom of the vertebrate ladder there were a number of suboccipital nerves, now undeveloped in living vertebrates as indicated by their vestiges in such elasmobranchs as *Heptanchus* (Daniel, 1922). In living vertebrates of a low order, however, the motor element subsequent to the vagus is furnished by the suboccipital and first one or two of the spinal nerves, which join to form the hypobranchial nerve, supplying the trunk musculature between the coracoid and lower jaw. In the higher vertebrates this becomes the hypoglossal (XII) nerve, with root situated endocranially.

Spinal nerves. The true spinal nerves of vertebrates have maintained a most uniform pattern. Each body segment has a pair of dorsal sensory roots, and a pair of motor roots from the ventral part of the cord. Fundamentally the former follow the myosepta and the latter the myomeres, and so come off of the cord in alternating order. Each root, both sensory and motor, divides, sending a dorsal ramus above the lateral line and a ventral ramus below. The two roots remain distinct in the lancelet, chiefly so in the lamprey, and to some extent in various elasmobranch embryos; but in vertebrates of higher organization there is fusion of each sensory with its corresponding motor branch, the connection beginning peripherally and progressing centrally (Allen, 1917). In these

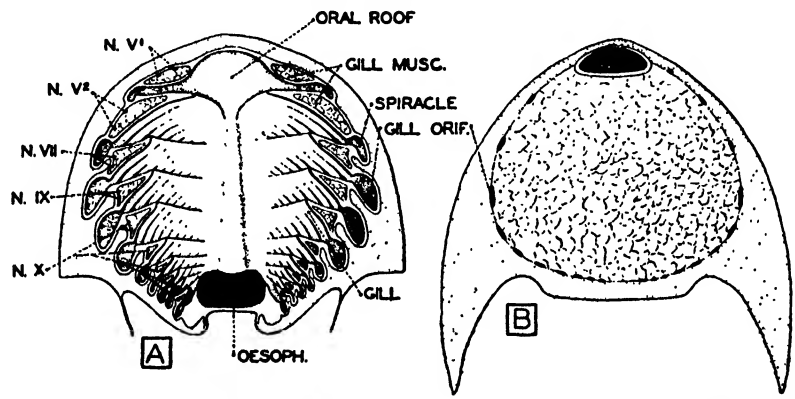

Fig. 1. (A) Horizontal Section through the Oral Region of Kiaeraspis, Showing Assumed Position of Gill Structures; (B) Ventral View of the Cephalic Shield of Cephalaspis Showing the External Branchial Apertures
After Stensiö

the result attained is that there is junction of the sensory with the motor root, and a redistribution of the fibers, so that upon each side the dorsal ramus of the spinal nerves contains both sensory and motor fibers, and the same is the case in the ventral ramus. It should be stressed that this plan of dorsal ramus above the lateral line and ventral ramus below is invariable in vertebrates. Later, in vertebrate history, there was experienced a tendency for the division of the ventral ramus into a lateral and a ventral branch, in accordance with division of muscular groups, but this was secondary.

Nerves to appendages. Whereas the distribution of the dorsal rami of the spinal nerves is relatively uniform, that of the ventral rami is affected by the presence of the appendages. It has been found (Howell, 1933) that the primary neural plan for the limbs is for the anterior nerve or nerves to supply a system of protractor muscle slips, for advancing the appendage, while the more caudal nerves supply a retractor muscle series, for retarding the fin. This plan of appendicular control, here called the primary basic arrangement, was not suited to an active, free-swimming vertebrate, and accordingly there was experienced a rearrangement of the muscular units, with consequent effect upon the distribution of the nerves. More specifically there was assumed a secondary basic plan, in which the protractor and retractor muscles divided into extensor and flexor elements. Thus each nerve to the appendage eventually acquired a dorsal, extensor branch and a ventral, flexor branch, simulating the lateral and ventral branches of the other trunk nerves, but independently developed. This occurred so far back in the phylogeny of the higher vertebrates that it is an invariable character of all living, terrestrial forms with limbs, at least in the higher members of which the extensor nerves of the pectoral appendage are always readily distinguishable from those of the flexor series.

Number of brachial nerves. The number of spinal nerves contributing to the innervation of the anterior limb is extremely variable in the lower vertebrates, there being 3 in some amphibians, reptiles and birds, and, among the fish, 55 or more in *Trygon*. Even the posterior cranial nerves may be involved in some of the skates. The number varies, of course, with the number of myotomes concerned in the formation of the appendicular musculature. In a fin with broad base the number may readily increase or decrease, but it is likely that after the base of the fin has once become constricted, following increase of motility in the axial direction, the number remains constant within very narrow limits in any particular phylum. Such constriction of the limb base gathers the nerves into a narrow area. The primitive position of the brachial nerves, and hence of the myotomes from which the brachial muscles arose, would appear to be directly posterior to the hypobranchial series. Great alteration in the position of the brachial nerves is relatively rare, but is extreme in some birds and particularly in reptiles, for as many as 76 cervical vertebrae occurred in some plesiosaurs.

Formation of plexuses. The morphology of plexus formation, or anastomosis of the nerves supplying the appendages, has never been fully explained, but it appears to have occurred in correlation with the crowding of muscles of plurisegmental derivation into a narrowed fin base. The less plausible of two hypotheses is based on the supposition that at one time there was a general, peripheral anastomosis between spinal nerves, such as occurs so extensively in living Holocephali, but that these connections were, in higher forms, abandoned except in the case of the ap-

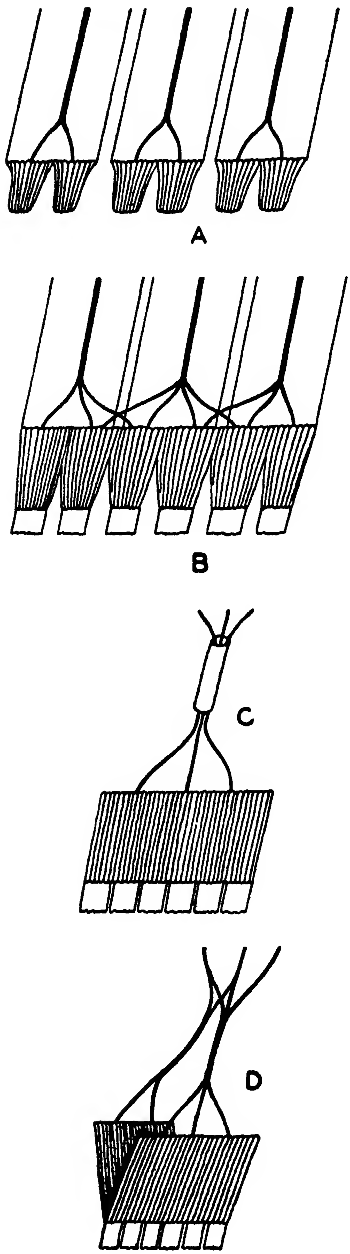

FIG. 2. DIAGRAMMATIC REPRESENTATION OF MANNER IN WHICH MULTISEGMENTAL MUSCLES TO APPENDAGES WERE PROBABLY DERIVED FROM BIPARTITE, SEGMENTAL MUSCLE BUDS; ALSO SHOWING MOTOR INNERVATION AND PROBABLE MANNER IN WHICH NERVE PLEXUSES WERE BROUGHT ABOUT THROUGH CONCENTRATION OF NERVE BRANCHES WITH INCLUSION IN A COMMON SHEATH, AND FINALLY SPLITTING OF THE MUSCLE COMPONENT

pendicular nerves, in which the crowding or plurisegmental character of the components proved favorable for the retention, or at least the proximal migration, of this feature. The more likely explanation of the formation of the limb plexuses lies in the fact that some of the appendageous muscles of relatively small size are derived from a number of myomeres. Hence the nerves supplying any one such muscle are closely grouped and parts of them may come to be enclosed in a single sheath, forming a "cord." Later a second muscle layer splits off from the first, in response to functional needs, and the nerve fibers to it will tend to split from the parent nerves in a fashion suggested in figure 2, finally resulting in a typical plexus formation.

Reflex action. The functioning of the nervous system is a subject entirely too complex, with many of its details too poorly understood, to discuss at length here, but a few salient facts should be mentioned.

In final analysis all action is reflex in character. The critical difference between the activities of an animal of low organization and of man lies in the fact that in the latter case the motor responses are more elaborate, complex and less predictable. In a simple type of reflex arc a sensory impulse, such as arises from pressure upon the sole of the foot, is received and transmitted by a sensory neuron to the spinal cord. It is transferred through a synapse to a short associational neuron, which in turn transmits it to a motor neuron in the ventral horn of the gray matter of the cord, from which it travels by way of an axon in the motor root to the peripheral effector (muscle), and a response results. In this particular case the receptor is proprioceptive (muscle sense) and the mechanism may be confined to half of a single body segment. Complexity may be introduced into the arc by the branch-

ing of the axon of the associational neuron, the impulse then being transmitted to a number of motor neurons at the same or at other levels, and upon the same or opposite side, of the cord.

Particularly in low forms of vertebrates if the spinal cord be isolated from the brain then the limbs still have a complete nervous equipment for the performance of the above type of action, the degree of perfection of coördination depending upon the development of associational connections. To be of practical use in progression reflex action must be of a rhythmic character, involving successively the excitation of a group of muscles effecting prime movement, and then a group of antagonist muscles for recovery, with fixation muscles contributing. The rhythm may be simple and concerned with the flexors and extensors of a single limb or may be highly complex, bringing into play not only other limbs to effect diagonal progression or simultaneous action but bending of the entire body. Whether an animal shall leap like a kangaroo, gallop or trot is determined by the organization of the reflex arcs.

Experiments in this field have been numerous but only a few instances will be cited. Snyder (1904) found that in a spinal urodele (*Batrachoseps*) walking is due to impulses originating in the periphery, such as those of stretching or of impact. I have found that in an alligator electrical stimulation of a single fore limb muscle (not its nerve, necessarily) may be sufficient for protractive and retractive movement not only of that member, but of the other limbs as well, chiefly the opposite and diagonal appendages, although this was not well coördinated. Sherrington (1920) found that in a spinal dog resting on its back, if one hind paw be pressed that leg will be flexed at hip, knee and ankle, and if the stimulus be strong the opposite limb will be extended. But if both hind paws be pressed then both limbs are simultaneously flexed and there is no trace of extension. The facility of spread from one side of the cord to the other (commissural pathways) was found to be very dissimilar at different levels, and motor mechanisms which are yoked together are (in the dog) for the most part of an asymmetrical kind, as the extensors of one side with the flexors of the other. In many animals it was found less easy to excite movement of one fore limb from the other than one hind limb from the other.

Newly initiated actions are dependent upon new connections established by associational neurones. When one learns a difficult feat of legerdemain it involves not primarily the development of muscles but the establishment of new reflex pathways, and it is probable that in certain parts of the nervous mechanism new connections can always be established through education (Edinger, 1911).

But reflex action can be instituted through various sensory pathways other than proprioceptive—by touch, temperature, pain, taste, smell, hearing, sight. The higher the animal in the scale of development the more complex are the motor responses, involving as they often do reflex pathways through the brain. Although many types of sensory impulses play on the nervous system of primitive forms the motor side of the reflex arc is poorly developed and the possible types of responses are few. Such limitations in a particular phylum must be of the utmost fundamental importance to its potentialities for progressive evolution.

In the white matter of the cord are tracts of sensory nerve fibers ascending from the different levels of the cord to the brain (afferent systems) and motor axons (corresponding efferent systems) constituting descending tracts from the brain effecting both voluntary and involuntary

action. In the lower vertebrates the former predominate, while in the higher there is an increase in the latter (e. g. development of corticospinal tracts in the Mammalia), showing the increasing importance of the brain in controlling reflex activity and the further elaboration of the motor side of the reflex arc.

Posture. Physiologists like to think of tone in the striated muscles as postural in quality inasmuch as it enables the organism to resist the force of gravity. A urodele must control tone in the extremities through very simple reflex arcs involving only the axis of the nervous system. In higher forms an elaborate reflex mechanism for tone control is developed in the mid-brain. This was first demonstrated by Sherrington. After decerebration of mammals there is rigidity of the extensor or anti-gravity muscles of the limbs. Curiously enough this is not true of the sloth, a mammal in which the flexor muscles normally support the body in an inverted posture. Here the flexor muscles of the limbs show increased tonus after removal of the forebrain. This postural reflex, maintained and influenced by many types of sensory stimuli, particularly proprioceptive and vestibular, controls the habitual positions which an animal maintains. Thus the horse or elephant is able to sleep standing up. Bagley and Langworthy (1926) detected the early control of tone through the mid-brain in reptiles, for they found in an alligator that extensor rigidity followed an attempt by the decerebrate animal to walk. A high type of terrestrial life is utterly impossible without an elaborate development of the anti-gravity reflex and its further differentiation through arcs involving the brain was one of the several prerequisites acquired by that group of reptiles which supposedly gave rise to the Mammalia.

The Rolleston-Fürbringer Theory. This hypothesis postulates that each motor nerve bears a constant relation to its corresponding myomere throughout both phylogeny and ontogeny. This is believed by the majority of present day anatomists to be a fact, although there have been a number of investigators (Cunningham, Leche, Westling, Kohlbrügge, Romer, Edgeworth, Wheeler and Adams) who consider that exceptions occur. In other words each muscle slip, no matter how far it may wander during evolution from its original position, will always be innervated by the motor nerve of its original segment. Apparent exceptions have almost always proved to have been attributable to a misunderstanding in interpreting conditions. One frequent misconception is to the effect that the numerical position of the segment by which the axon leaves the cord is the essential criterion. This need have no bearing on the matter, however, for the important point is the position of the motor nucleus, so the statement should be modified to read that the relation of a muscle to its original motor nucleus in the central nervous system remains forever constant.

Law of neurobiotaxis. This law, advanced by Kappers, postulates that in the course of phylogeny the neurons of the motor nuclei tend to migrate in the direction from which they habitually receive their stimuli. This has been pretty well demonstrated for the brain but very little work with this in mind has been done on the spinal cord.

Possible migration of the motor nuclei in the cord. The extensor muscles, say, of the arm in man arise usually from sp. nn. 5 to 8, and the motor nuclei of these nerves (axillary and radial) lie in the adjoining part of the cord. But nerves to other groups of muscles (flexors) arise from these roots as well, so the nuclei of different muscles and muscle groups are packed within the ven-

tral horn of gray matter in aggregations. Whether the latter are always of a concencentrated character or at times are esssentially diffuse or discrete is a matter yet to be determined. At least the position of the nuclei is remarkably constant within the class Mammalia, but there is some variation, both ordinal and individual. Thus, although the radial nerve usually arises from the sixth to eighth cervical nerves, occasionally it comes from one root higher or one lower. In other words it seems that its motor nucleus occasionally wanders fractionally either above or below its usual position. Although it is believed that the difference in the brachial neural plan of a low urodele, for instance, and a mammal is attributable largely to basal ancestral dissimilarity, it is not unlikely that it is partly due to the migration of the motor nuclei. Thus it is conceivable that a muscle slip now innervated by the fifth cervical nerve in a mammal may have been derived from one segment higher or (less likely) lower in an ancestral form.

Plurisegmental innervation. Not only may a single small muscle have been derived from a number of myomeres, as elaborated elsewhere, but it has been demonstrated that in fish this may involve a variably slight degree of overlap of the segmental elements (Braus, 1909; Goodrich, 1910; Müller, 1911). Some (Goodrich, 1930) have considered that this involves not a wandering of a nerve to muscle fibers of adjoining segments but rather to a migration of fibers from their own to neighboring myomeres. In seeming controversion of this interpretation, however, is the fact that in mammals and in the frog at least the same muscle fiber may be supplied by motor twigs from two, or even three adjoining neuromeres (in Hines, 1927). It has never been explained how this could be so and the peripheral nervous system still retain its astonishing conservativeness in other respects throughout so many millions of years.

GENERAL CONSIDERATIONS OF THE MUSCULAR SYSTEM

Many of the basic features of the muscles have been touched upon in the last section, but there are additional details needing consideration.

Somatic and branchial musculature. All striated musculature (except cardiac) is divisible into these two groups, although the division can not be made on hard and fast lines except on the basis of innervation. For the most part somatic muscles have muscle spindles (for proprioceptive purposes) while branchial muscles do not; but there are exceptions, for these have been found in the m. pterygoideus externus and the m. masseter of the rabbit (Cipollone, 1897) and in the latter muscle of the fetal pig (Cuajunco, in Hines, 1927). They have not been found in the extrinsic eye muscles of the dog, fox, cat, hare, rat, horse, and domestic pig (Cilimbaris, 1910). Occasionally even the criterion of gross innervation fails definitely to distinguish somatic from visceral muscles (spinal innervation of m. trapezius) and recourse must be had to experiments involving degeneration of the motor nuclei. In general only somatic muscles are considered to have segmental innervation, but actually the branchial musculature also conforms basically to a segmental arrangement. The latter, primarily concerned with the pharyngeal mechanism, becomes partially subcutaneous and invades the field of somatic musculature. The basic arrangement of the branchiomeric division has already been mentioned.

Basic segmental features. The original plan of vertebrate trunk musculature, well illustrated by cyclostomes, involves a series of segmental muscles each of which is

separated from the muscles of adjoining segments by myocommata or myosepta. The axially directed muscle fibers of each segment are basically divided into a dorsal division, above the lateral line on either side of the midline, and a continuous latero-ventral division below; this constitutes the primary muscular plan. It is a primitive scheme, suited to a low vertebrate that can bend with equal facility in any direction—the essentially vermiform type of control.

In this plan the myosepta are virtually transverse and usually gently curved. Unlike the situation in mammals, most of

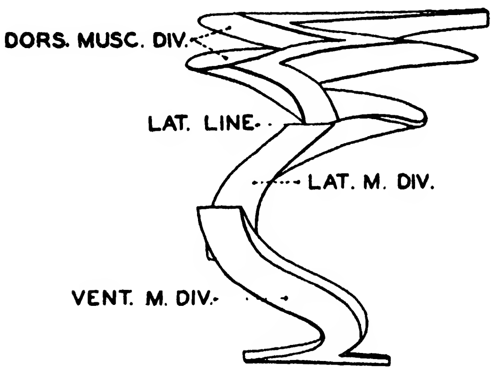

FIG. 3. MODEL OF MYOMERE OF A SELACHIAN (SQUALUS)
Modified from Langelaan and Daniel

whose muscles have one end solidly anchored on bone, in the primitive state the fibers at both ends are attached to yielding connective tissue. Accordingly there was originally a tendency for some of the groups of fibers to pull certain parts of the myosepta in a forward and others in a backward direction, as a result of specialized action of the groups concerned. This would have a contortional effect upon the myosepta, and in consequence some parts would have an anterior and others a posterior inclination, as suggested in the given diagram of a myomere of a shark (fig. 3). Presumably the swifter the fish (i.e. the stronger the muscle action) the more tortuous the pattern of the myosepta.

Adoption of trunk muscle divisions. A result of the latter is the secondary basic plan of vertebrate musculature involving (a) the original dorsal element above the lateral line, an extensor of the trunk, thick because located near the notochord and having short leverage, (b) a ventral component, split off from the original latero-ventral musculature to form a flexor of the trunk, tending to be thinner than the extensor for the reason that it is located farther from the notochord and hence with longer leverage, and (c) a lateral muscle division below the lateral line on either side for horizontal flexure of the body. The development of this plan has been in response to the need, as evolution progressed, for movement in restricted planes, extension and flexion, abduction and adduction. The divisions most probably took place at the points where the angles formed by the alteration in the direction of the myosepta were most acute; actually such changes in the myosepta must have been the first indications of future muscular divisions. Variations in the relative size of the ventral and lateral divisions occur in accordance with the functional stimuli to which they have been subjected. And future lesser, or tertiary, divisions occurred at the point where there were minor flexures of the myosepta.

Basic plan of peripheral musculature. As explained in more detail in future sections the initiation of the fins is believed to have involved development of segmental, dermal scutes, to each of which was attached a muscle slip (fig. 4). As these scutes lengthened and a fin-like structure took form, the controlling musculature first aligned itself into a posterior, prime mover group, for retraction, and an anterior, antagonist group for recovery or protraction. This was the primary plan

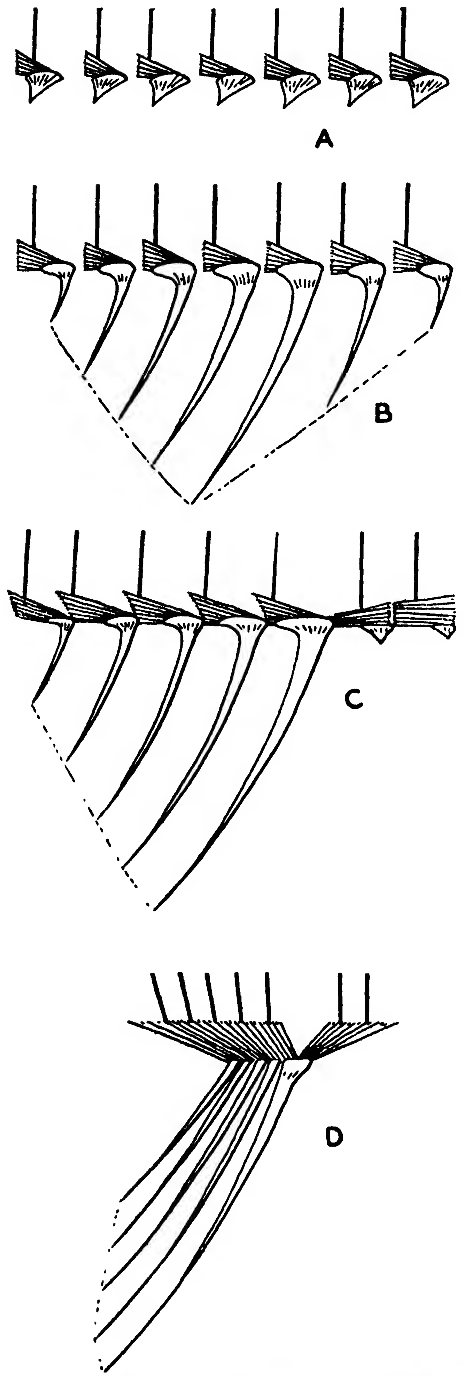

FIG. 4. DIAGRAMMATIC REPRESENTATION OF THE PROBABLE MANNER OF FIN MORPHOGENESIS FROM DERMAL ELEMENTS, SHOWING CONCRETION OF SEGMENTAL MUSCLE COMPONENTS AND THEIR MOTOR INNERVATION

and was followed in forms having the appendages composed of many segments (Selachii) by the stringing together of the individual muscle slips, as the base of the fin became contracted, into longitudinal series. The secondary plan involved a regrouping of the original protractor-retractor elements into extensor-flexor, elevator-depressor, or abductor-adductor musculature. This could be done according to any one of several schemes. All myomeres might contribute equally to the dorsal and ventral groups of fin musculature, as appears to have been the case in many teleosts, the anteriormost brachial muscle components may contribute to the formation of the cranial part of the ventral group only, as apparently is the case in *Polypterus* and in more exaggerated degree in elasmobranchs, or there might be other schemes. From this point on, however, the muscular differentiation varied in pattern with the diversity of the stimuli encountered in different groups of fish, so that variation is great.

GENERAL CONSIDERATIONS OF THE SKELETAL SYSTEM

As already stated bones are either membranous (dermal) or cartilaginous in derivation. The two occasionally fuse, the cartilage then showing a tendency to disappear through absorption. Cartilage (and therefore bone) can occur wherever there is the proper stimulus, and this is usually muscle stress, in myosepta and between muscle groups. Whether cartilage remains in that state or becomes bone depends upon several factors, some of which are obscure. On the whole it is usual for cartilage to predominate in extremely low vertebrates and in those sorts in which the muscle action is weak or distributed through broad attachments (urodeles). There is much group difference, however, and there is no reason clear to us why a

shark should be largely cartilaginous while such teleosts as the shad should develop slender bones in practically every conceivable situation.

As far as one can see cartilage is the same whether occurring as a costal, appendageous, or branchial element, not a primary necessity but something developed where need arises, just as connective tissue occurs in a variety of situations. It may develop a joint, enclosed by an articular capsule, whenever there is need for one, the new element being preceded by a process projected from the old, and such cartilages (or bones), at least elsewhere than the skull, usually constitute the anchorage of functional groups of muscles. Occasionally, however, there occurs cartilage purely for stiffening purposes (extrabranchials). A cartilage (or bone) will persist as long as it functions as an anchorage for muscles. It will have a movable joint for attachment to other cartilages as long as motility is advantageous, but if structural strength become a desideratum then the movable joint will eventually be replaced by an immovable suture.

A bone constituting a single phylogenetic element will usually have but a single primary center of ossification. Secondary centers in the nature of epiphyses with sutural attachment may develop from the transmission of weight (pressure-epiphyses) or where muscles of great power have restricted attachment (traction-epiphyses). A third type (atavistic epiphyses) are the degenerate remains of formerly functional osteologic elements (Parsons). The tendinous attachment of a strong muscle may be marked only by a slight rugosity, or actually by a fossa, if the position of the bone give it an efficient angle of leverage, or if the latter be not the case, then the leverage will be obtained by the development of a crest or process. In many cases the formation of the latter is not so much an attribute of the bone itself as calcification at the junction of tendon and bone, stimulated by strong action; hence a process can be more strictly ontogenetic than phylogenetic. If sufficiently long continued, however, and sufficiently advantageous, it apparently may become, to a considerable extent, a phylogenetic character (spine of the scapula).

It should be mentioned that whereas most cartilages originally were a reflection of muscle stress, bones eventually conform largely to the mechanical exigencies of the organism, being robust or slender, long or short, and with articular details according to several factors other than those purely muscular. In final analysis, however, and broadly stated, osteological details reflect myological conditions, while these and neurological features are interdependent. Muscle preceded bone and a neural motor mechanism could never have been independent of muscle. Each is correlated with the other and an understanding of one can not be obtained without a consideration of all three.

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ON THE RATE OF OXYGEN CONSUMPTION BY TISSUES AND LOWER ORGANISMS AS A FUNCTION OF OXYGEN TENSION

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I

THE information dealing with the rates of O_2-consumption by tissues and lower organisms as function of O_2 tension in the surrounding media was summarized up to 1914 by Warburg (1914). Since then numerous data of a quantitative nature have been obtained, but as far as the writer is aware, no attempt to summarize the recent, perhaps more important, measurements has been made save that by Hyman (1929), who was interested in the matter through phylogenetic and ecological considerations. In view of the theoretical equations developed in recent years attempting to describe the rate of O_2-consumption as a function of O_2 tension (Warburg and Kubowitz, 1929; Shibata and Tamiya, 1930; Gerard, 1931; Roughton, 1932), and in view of the fact that the existing data are presented in very many diverse ways so that they are not readily comparable, it was deemed desirable that a quantitative summary and interpretations of the more recent work on the subject be made.

While it is undoubtedly true that in many cases the rate of O_2-consumption is independent of O_2 tension for the range tested, it is equally true that in a great number of cases definite relations exist between the two; and the possibility still remains that if the lower limits of the ranges of O_2 tension tested were extended, provided no irreversible changes occur in the respiring material, the rates which are considered independent of O_2 tension in many forms may prove to be dependent. In this account, we shall limit ourselves only to the cases where a definite relation exists between the two.

With a very few exceptions where the rate of O_2-consumption is directly proportional to O_2 tension, the type of relation obtained is hyperbolic; that is, the rate of O_2-consumption varies rapidly with O_2 tension at low concentrations, less so at higher concentrations, and a point is eventually reached where further increase in O_2 tension produces little or no effect on the rate of O_2-consumption, the tension at which the curve approaches saturation being the "critical pressure."

In the following treatment, all data (with one exception) were obtained from the numerical determinations given in the original articles, and all terms were converted into comparable units wherever possible. Thus the expression of O_2 tension in terms of percentage, in cc. O_2 per cc. water, cc. thiosulfate per cc. water, per cent saturation, etc., have all been converted into mm. Hg. In many cases the correction for vapor pressure was not specified, and it was assumed that such a correction was made. The error so introduced is not very serious, however. Instead of a percentage, the rate of O_2-consumption A, is expressed in terms of cc. of

O_2 consumed per hour per gram dry weight. In case dry weight was not given, "fresh weight" or "individual" is substituted. A is used in this paper as a general term designating the rate of consumption of O_2 expressed in cc. O_2 per hr. per gm. dry weight or fresh weight, or per individual. It therefore includes the Q_{O_2} of Warburg. A_0 is the maximum rate. In the experiments where the respiring material was kept in a closed container, and was allowed to reduce the O_2 tension in the surrounding medium by virtue of its own respiratory activity, and the amount of O_2 left in the medium was plotted against time, the data were recalculated in terms of amount of O_2 consumed as a function of O_2 pressure.

II

While it is not the purpose of the present account to review the various methods used in ascertaining the rate of O_2-consumption as a function of O_2 tension, a brief résumé is not out of place.

In general, the technics may be divided into two types. One of these is that of placing the respiring material in an enclosed system with a known initial concentration of O_2. The rate of consumption of O_2 is then followed either manometrically or by titrating the surrounding water as the tension in the system is reduced through the activity of the respiring material. While this type of method has its advantage over the one to be discussed below because the data in this case are obtained on the same material and therefore are not susceptible to variations arising from using different samples, it has many disadvantages. Since in such experiments the duration is usually over a period of several hours, the accumulation of waste material, especially of CO_2, change of pH of medium, lack of adequate stirring, and "adaptation," among others, may cause errors in measurements.

The second type of technic consists in subjecting the respiring materials for short intervals to gas mixtures of various O_2 tensions and comparing the rates with that of the control experiment at a given O_2 tension (usually that of the air). While this type of technic is relatively free from the objections mentioned in connection with the first type, it is not entirely satisfactory since the rate of O_2-consumption by different samples of material may not be strictly comparable, and since the O_2 tension in the surrounding medium is the mean tension from the beginning of the experiment to the end. Where the amount of O_2 consumed during the experiment is relatively large, as is necessarily the case where direct analysis of the gas is made, the uncertainty in expressing the O_2 tension is considerable.

In both cases, save where the CO_2 produced during the experiment was removed by suitable means, serious errors may arise from the effect of CO_2 on the rate of O_2-consumption (cf. Root, 1930). And except where the respiring materials are suspended in a gas medium, errors may result from insufficient stirring of the water surrounding them. The new technic of Warburg and Kubowitz (1929) was designed especially with the last point in view, but the high speed at which the respirometers are rotated may introduce additional complications due to possible injury to the respiring materials.

The relative merits of the methods used in the various accounts should be kept in mind in going through the discussions given in the following sections.

III

Without going into theoretical considerations, we shall, for convenience and conciseness, treat the relationship existing between the rate of O_2-consumption and O_2 tension by the equation:

$$A = \frac{P}{K_1 + K_2P} \qquad (1)$$

in which A represents cc. O_2 consumed per hour per gram dry weight (or units proportional thereto); P, the O_2 tension in mm. Hg.; and K_1 and K_2 are constants.

This equation not only takes into consideration the hyperbolic type of relation, but can be made to express all three empirically determined types of relationship existing between O_2-consumption and O_2 tension. For, if K_1 is comparatively much larger than K_2P, A is approximately equal to P/K_1 which is descriptive of the small number of data where the rate of O_2-consumption is directly proportional to O_2 tension. Conversely if K_1 is very small compared to K_2P, A may be considered a constant, and this is descriptive of the cases where the rate of O_2-consumption is apparently independent of O_2 tension.

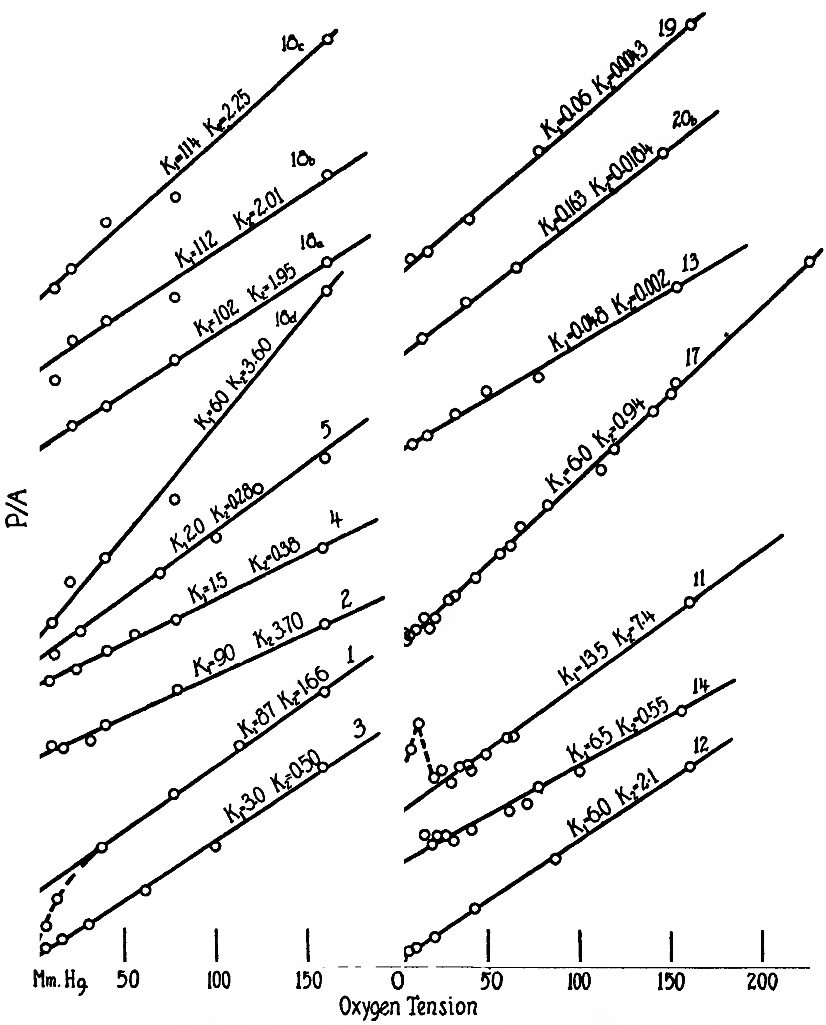

FIG. 1. A/P IN ARBITRARY UNITS IS PLOTTED AGAINST P, THE PARTIAL PRESSURE (CONCENTRATION) OF OXYGEN, IN MM. HG., A BEING THE RATE OF O_2-CONSUMPTION

The intercepts (K_1) and the slopes (K_2) of the lines are given along with the curves. The numbers attached to each curve refer to the material used, as listed in Table 1.

If equation (1) is a fair description of the relation existing between A and P, by

plotting P/A against P one should obtain a straight line with K_1 as its intercept and K_2 as the slope. Twenty-four different sets of data are so plotted in Figs. 1 and 2. attached to each line is the index of the object used, which is the same as that given throughout the text and in Table 1. The constants, K_1 (the intercept) and K_2 (the

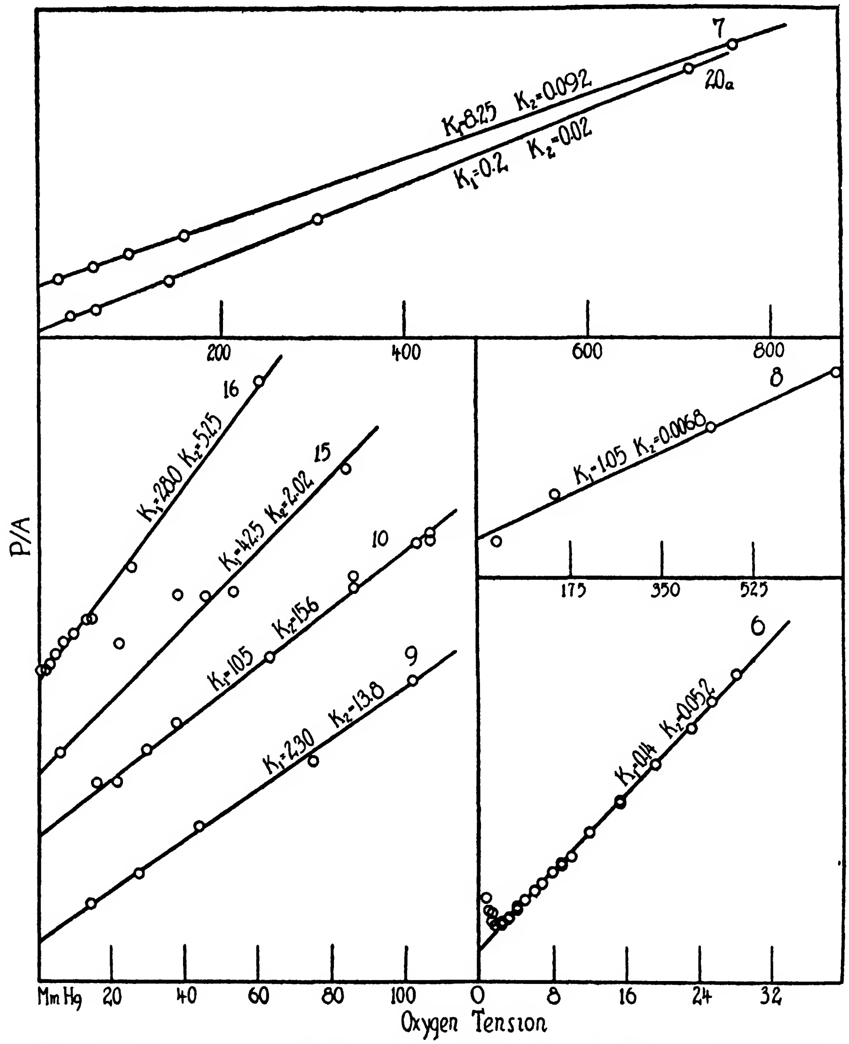

FIG. 2. A/P IN ARBITRARY UNITS IS PLOTTED AGAINST P, THE PARTIAL PRESSURE (CONCENTRATION) OF OXYGEN, IN MM. HG., A BEING THE RATE OF O_2-CONSUMPTION

The intercepts (K_1) and the slopes (K_2) of the lines are given along with the curves. The numbers attached to each curve refer to the material used, as listed in Table 1. The points for curve 15 were obtained at temperatures ranging from 16.5 to 23°. (See text.)

All the points are taken from original data except those for curve 16, where the points were taken from curve D in Fig. 3 of Dolk and Van der Paauw (1929). The number slope), are also given along the lines. Thus Figs. 1 and 2 are not only a graphic presentation of the validity of the application of equation (1), but are also a dia-

TABLE I

A summary of the essential points for the accounts mentioned in section III. The value of A for any value of P may be obtained through the relation $A = P/(K_1 + K_2P)$

	MATERIAL USED	METHOD	TEMP. °C.	A_0 Observed	A_0 Calculated $(1/K_2)$	RANGE OF O_2 TENSION *mm.Hg.*	CRITICAL TENSION *mm.Hg.*	K_1	K_2	AUTHOR
1	Leaves of *Hypnum triquetrum*	Objects enclosed in jars: evacuated and then proper mixtures of gas introduced. Respired gas extracted and analyzed	25	0.460	0.6	7.22–158.5	(158.5)	87.0	1.66	Chevillard, Hamon, Meyer and Plantefol (1930)
2	Fragments of potato tubers		25	0.237	0.27	8.8 –159.0	(159 0)	90 0	3.70	
3	Fragments of turnip		25	1.9	2.0	7 0 –158.0	55 0	3.0	0.50	
4	Fragments of mushroom		20	2 6	2.6	8 05–158.0	55.0	1.5	0.38	
5	Leaves of cress		20	3.5	3.6	10.8 –159.0	55.0	2.0	0.28	
6	Luminous bacteria	Thunberg-Winterstein microrespirometers	21[1]	17.4[1]	19.2	0 68– 28.1	22.8	0.140	0.052	Shoup (1929–30)
7	Fertilized eggs of *Paracentrotus lividus*	Manometric	—	9.56	11.0	0.0 –760.0	228.0	8.25	0.092	Drastich (1927)
8	Oxidation of cystine on charcoal	Warburg microrespirometer	40	—	—	36.0 –684.0	—	1.05	0.0068	Warburg (1928)
9	Puffer (*Tetraodon maculatus*)	Ege and Krogh respirometer. O_2 content of water was analyzed with Winkler method before and after contact with fish	20–21	0.0636[4]	0.07	14 35–102.0	100.0	230.0	13.80	Hall (1929)
10	Scup (*Stenotomus chrysops*)		20–21	0.063[4]	0.065	15.8 –107.0	70.0	105.0	15.6	
11	*Planaria agilis*	Worm kept in H_2O of diff. O_2 tension. Winkler method used for analysis	20	0.12[4]	0.135	6 5 – 62.5	159 0	135.0	7.4	Lund (1921)
12	Unfertilized eggs of *Arbacia punctulata*	Warburg microrespirometer	25	0.485	0.48	2.0 –160 0	40.0	6.0	2.10	Tang (1931)
13	*Azotobacter chroococcum*	New method of Warburg and Kubowitz	10	435.0	500 0	7 6 –152.0	110.0	0.048	0.002	Meyerhof and Schulz (1932)

14	Fertilized eggs of *Arbacia punctulata*	Warburg microrespirometer	25	1.7	1.8	13.0	–155.0	50.0	6.5	0.55	Tang and Gerard (1932)
15	Fragments of *Chironomus thummi* larvae	Warburg microrespirometer	16.5–23.0	0.400[4]	0.495	6.1	– 83.5	70.0	42.5	2.02	Harnish (1930)
16	Earthworm	Modified Krogh: worm supported in gas atmosphere	25	0.178[5]	0.190	0 0	–159.0	19.0	28.0	5.25	Dolk and Van der Paauw (1929)
17	Fertilized eggs of *Arbacia*	Eggs rotated in tonometer with proper gas mixture. Gas analyzed afterwards	18.2–20.2	1.0[3]	1 04	3 0	–224.4	20.0	6.0	0.94	Amberson (1928)
18	*Dixippus morosus*	Krogh microrespirometer	17	0.314[2,5]	0.40	9.5	–160.0	159.0	94.0[2]	2.45[2]	von Buddenbrock and von Rohr (1923)
19	Termites (*Termopsis nevadensis*)	Warburg microrespirometer	20	213 0[6]	230.0	6.1	–760 0	40.0	0.06	0.0043	Cook (1932)
20*a*	Yeast	Warburg differential microrespirometer	37	48 0	50 0	36.0	–712.0	100.0	0.2	0.02	Cook (1930–31)
b			37	48.0	55.0	11.5	–144.0	100 0	0.163	0.0184	

[1] Temperature and A_0 not specified. Figures taken from Harvey (1928).

[2] Average of 4 experiments.

[3] The value of 1.0 was arrived at from the data of Tang and Gerard where $A_0 = 1.7$ at 25° (μ assumed to be 16,000).

[4] cc./hr./gm. fresh weight.

[5] cc./hr./gm./individual.

[6] The value of 213 is reduced from the average value of 805 at 35° (μ assumed to be 16,000).

grammatic summary of the great majority of the recent quantitative data relating oxygen tension and rate of O_2-consumption by tissues and by lower organisms. A glance at these figures and Table 1 reveals the variety of materials studied, the ranges of O_2 tension used, and the constants for the different materials.

The set of data labelled from 1 to 5 are taken from Chevillard, Hamon, Meyer, and Plantefol (1930). These workers subjected leaves of *Hypnum* moss (1), fragments of potato (2), turnip (3), and mushroom (4), and leaves of cress (5) to chambers containing mixtures of gases the O_2-concentration of which varied from 7.0 to 159 mm. Hg. After a period in a thermostat kept at 20 or 25°, the gases were extracted from the chambers and analyzed. They found that a reduction in O_2 tension affects the rate of CO_2 production as well as O_2-consumption; but the two are affected differently in such a manner that the ratio of CO_2 production to O_2-consumption (Respiratory Quotient) is raised as the concentration of O_2 is lowered. The experiments were not performed beyond a partial pressure of 159 mm. Hg., and in the case of *Hypnum* and potato the critical concentration is evidently beyond the highest pressure tested. For the rest, the critical pressure is at about 58 mm. Hg. The slight deviation of the points at the low pressures in Curve 1 is probably due to technical errors.

In his study of the rate of oxygen consumption of the luminous bacteria as a function of oxygen tension, Shoup (1929–30) concluded that beyond a critical pressure of 22.8 mm. Hg. the rate of O_2-consumption remains unaltered as the oxygen tension in the medium is changed. No mention was made in the paper of the temperature nor of the absolute rate. In Table 1, the temperature and A_0 were taken from Harvey (1928). Shoup is of the opinion that his curve is similar to that for adsorption of gases on solid surface and that the mode of action of O_2 with the respiratory enzyme of the bacteria is the same as that of surface catalysis in heterogeneous chemical systems. His data are plotted in graph 6. It is seen that a straight line fits all except the points below a pressure of about 1.5 mm., where deviation occurs. In view of the uncertainties of measurements at such small concentrations of oxygen, too much significance need not be attached to this apparent deviation.

In connection with the study of the mechanism of fertilization, Drastich (1927) made some observations on the relation of oxygen tension and the rate of oxygen consumption in the fertilized eggs of *Paracentrotus lividus*, using the manometric method, without mentioning the temperature of the experiment. The points are plotted on the curve numbered 7.

Curve no. 8 is for the catalytic oxidation of cystine on charcoal surface at 40° as measured by Warburg and Negelein (1921). The points were taken during the first 21 minutes of reaction. This set of data was plotted here merely for comparison between chemical catalysis and biological oxidations. It is noticed that like the data for biological oxidations, the points can be fitted with the same equation.

Hall (1929) studied the rates of oxygen consumption of three types of fish: *Tetraodon maculatus* (Puffer), *Stenotomus chrysops* (Scup), and *Opsanus tau* (Toadfish). The procedure consisted in ascertaining the O_2 content of the water, with Winkler titration, before and after passing through the tank containing the fish. While he found a hyperbolic relation in the first two cases (curves 9 and 10), a straight line function was obtained with the toadfish. He correlated the findings with hemoglobin content and the speed of movement of the fish. The toadfish, which is the most

sluggish and has the least amount of hemoglobin, has not only the lowest absolute rate of O_2-consumption among the three, but the rate is also directly proportional to oxygen tension up to 100 mm. Hg.

Curve 11 is obtained with *Planaria agilis* by Lund (1918) using the Winkler method. Instead of having the worms in a closed container and allowing the O_2 tension of the medium to decrease with time as is usually done with the Winkler technic, the animals were subjected to samples of water of varied O_2 tension up to 410 mm. Hg. The deviation of the points at lower pressures from the straight line is probably due to errors in measurement.

Tang (1931) and Tang and Gerard (1932) secured data for the oxygen consumption-O_2 tension relationship in the fertilized (14) and unfertilized (12) eggs of *Arbacia*. In both cases they found a hyperbolic relationship, with critical tensions occurring at 50 and 40 mm. Hg. respectively. Unpublished data obtained by the same authors with cytolyzed eggs show that the rate for cytolyzed eggs, as that of the intact ones, bears a hyperbolic relationship to O_2 tension.

By the use of the new method of Warburg and Kubowitz (1929), where the respirometer was shaken at 540 oscillations per minute so that diffusion through the liquid medium is not a factor, and by the use of cells (*Azotobacter*) the diameter of which is such that diffusion through tissue is not a source of error, Meyerhof and Schulz (1932) demonstrated a hyperbolic relation between the rate of O_2-consumption and O_2 tension, with a critical pressure of 110 mm. (curve 13). These authors are of the opinion that at lower O_2 tensions the "respiratory ferment" is not entirely saturated but that part is dissociated, and the hyperbolic curve obtained is to be expected from the dissociation of the "ferment."

Curve 15 represents the data obtained by Harnish (1930) with finely divided fragments of larvæ of *Chironomus thummi*. This author had previously found that the rate of O_2-consumption of the intact animal was dependent on the oxygen tension of the surrounding medium. The experiment with fragments of the larvæ was planned to show that the relationship is a real one, and is not an artefact due to insufficient diffusion of O_2 through the tissues. The temperatures of the individual experiments varied from 16.5° to 23.0°, hence the data are not as exact as desired, and the points are not expected to fall on a straight line; the data are given here merely to show that insufficient diffusion of O_2 through the tissue is not a factor in this case and, like many others, a hyperbolic relationship still exists between O_2 tension and the rate of O_2-consumption.

Dolk and Van der Paauw (1929) studied the rate of O_2-consumption as a function of O_2-tension in the normal as well as in CO-treated earthworms. They found that in the normal worm, the part of the curve below the critical tension of 19 mm. Hg. is similar to the dissociation curve of hemoglobin. With CO-treated worms, the critical tension came at 57 mm. Hg. Their opinion is that hemoglobin in the blood of the worm plays an important rôle below the critical tension. Attempts to transpose the figures in their table were not successful and the points for curve 16 were taken from curve D, Fig. 3, of their paper.

Amberson (1928) studied the relation of oxygen tension and the rate of respiration in *Paramaecium* and the fertilized eggs of *Arbacia* by subjecting equal amounts of the cells in tonometers which were partially filled with water in equilibrium with air and with O_2–N_2 mixtures of varied proportions. After several hours during which the tonometers were in constant rotation, the gases were extracted and

analyzed. Although the data obtained with *Paramaecium* showed a slightly decreased rate of respiration with decreasing O_2 tension, the lower limit of the experiment was too high to bring to light the true relationship which may exist between the two. The data on the fertilized *Arbacia* eggs are more comprehensive, and it was found that while above the critical pressure of 20 mm. Hg. the rate of respiration is independent of O_2 tension, below that pressure, the rate falls rapidly with falling tension. His data seem to indicate that as in the case of plant tissues, the R. Q. increases with falling oxygen tension. Since the absolute maximum rate was not given, the value of 1.7 found by Tang and Gerard (1932) at 25° was reduced to 1.0 at 18° (assuming a μ of 16,000) and was adopted as a rough approximation. K_1 and K_2 were calculated on this basis.

Von Buddenbrock and von Rohr (1923) observed the rate of respiration of *Dixippus* in groups of three or more. The rate was studied as a function of temperature, O_2 tension, and CO_2 concentration and of the combination of the first two factors. Four sets of data with three insects each were obtained at different O_2 tensions and these are plotted as 18 *a*, *b*, *c*, and *d* in Fig. 1. The constants as well as the critical oxygen pressure of three sets (18 *a*, *b*, and *c*) agree fairly closely, while the fourth group (18 *d*) gave constants which are slightly different, but which are of the same order of magnitude as those found in the first three sets. The averaged values are given in Table 1.

Using yeast as material, Cook (1931) studied the variation in the rate of respiration and fermentation when the partial as well as the total pressure of O_2 were altered. It was found that while the rate of O_2-consumption is affected in both cases, the effects are not identical: a reduction of pressure as such induced a much greater change in rate of O_2-consumption than changing the concentration of O_2. Such a state of affairs was not found in the case of fructose. Only the two sets of data deal ing with the effect of changing of the partial pressure of O_2 on the O_2-consumption rate of yeast are given in the Figures (20*a* and 20*b*).

In a more recent paper, Cook (1932) ascertained the rate of O_2-consumption of termites (*Termopsis nevadensis*) in the range of partial pressure of O_2 between 6.1 and 760 mm. Hg., by means of the Warburg technic. The rate was found to be practically independent of O_2 tension down to 40 mm. Hg., when the curve fell rapidly with decreasing O_2 tension. The average absolute rate of oxygen consumption for 10 groups of 12 individuals each is 805 cc. O_2 per gm. per hr., at 35°. But the O_2 tension vs. O_2-consumption relation was obtained at 20°, and only the percentages are given. Assuming a temperature characteristic (μ) of 16,000, the rate at 20° in air may be taken as 213 cc. per gm. per hr. P/A is then calculated on this basis and the constants in Table 1 are computed accordingly. The points, with the exception of that taken at 760 mm. Hg. where a slight injurious effect was apparent, are plotted as curve 19.

The essential points in the accounts mentioned above are summarized in Table 1.

IV

In a very few cases, the data show that the rate of O_2-consumption is a linear function of O_2 tension and cannot be treated in the above manner. They are therefore given separately.

Amberson, Mayerson, and Scott (1924–25) studied the rate of O_2-consumption of the lobster (*Homarus americanus*) and *Nereis virens* using the Winkler method and allowing the animals to reduce the O_2 tension of the water through their own re-

spiratory activities. These authors obtained a straight line relation between log of O_2 tension in water and time, hence a linear relationship between the rate of O_2-consumption and O_2 tension from about 760 to about 76 mm. Hg. ("full" and "10 per cent saturation" respectively). It is to be remembered that while a single animal was used in the case of the lobster, 82 animals were used for the experiment with *Nereis*.

Using the same technic as that of Amberson *et al.*, Chen (1930) claimed to have found a linear relationship between O_2 tension and the rate of O_2-consumption in the Chinese freshwater crab (*Eriocheis sinensis*). This is true only for the range of 160 to 720 mm. Hg. ("21" and "95 per cent saturation" respectively). The rate fell rapidly and irregularly below 160 mm. Hg. The same may be said of the results of Nomura (1926) obtained on *Caudina chilensis* between the partial O_2 pressures of 20 and 133 mm. Hg.

Hall (1929) found a linear relationship between the rate of O_2-consumption and the O_2 tension of the surrounding water in the Toadfish, while such is not the case in the Scup and Puffer as mentioned above. The difference was attributed to the sluggishness and the lower hemoglobin content of the Toadfish.

Tamiya (1929) obtained a direct relationship between the rate of O_2-consumption and O_2 tension in *Aspergillus oryzae* from 0 to 509 mm. beyond which the relation fails to hold. An explanation of this observation was attempted later by Shibata and Tamiya (1930) in terms of the absence of cytochrome, and the influence of diffusion.

While linear relationship between the rate of O_2-consumption and O_2 tension of the media in the aforementioned cases may be entirely correct, technical errors such as insufficient rate of diffusion of the gas through the liquid medium as well as through the tissues, among other factors, must not be overlooked, especially in the experiments where such animals as the crab and lobster were used.

V

It is evident from the data collected that the hyperbolic equation

$$A = \frac{P}{K_1 + K_2 P}$$

holds true for most of the measurements dealing with the rate of O_2-consumption as a function of O_2 tension. This type of equation was first derived for the O_2-dissociation curve of hemoglobin by Hüfner and by Hill (see Barcroft, 1928) and for that of hemocyanin by Stedman and Stedman (1928), and Redfield (1930). Warburg and Kubowitz (1929), and later Shibata and Tamiya (1930), and Gerard (1931), arrived at a similar type of equation for cell respiration, based upon the assumption that the following reactions take place when O_2 is being consumed by the respiring material through the catalytic action of the intermediate substance I, which may be cytochrome, "ferment," or any other respiratory catalyst:

$$O_2 + I \longrightarrow I\,O_2$$
$$I\,O_2 + S \longrightarrow I + S\,O_2$$

when S, the substrate, is present in excess and if we are concerned only with the oxidation and reduction of I, the reaction may be simply represented by the scheme:

$$I + O_2 \rightleftarrows I\,O_2$$

Assuming further that A/A_0 is a measure of the relative concentrations of I and $I\,O_2$, their expression relating A/A_0 and P may be stated in the following manner:

$$\frac{n}{(1 - n)P} = K$$

in which $n = A/A_0$, or,

$$\frac{A}{A_0} = \frac{KP}{1 + KP} \qquad (2)$$

Transposing,

$$A = \frac{A_0KP}{1 + KP}$$

Letting $1/KA_0 = K_1$ and $1/A_0 = K_2$, we have:

$$A = \frac{P}{K_1 + K_2P}$$

which is similar to our empirical equation, and in which $1/K_2$ should be equal to A_0 and K_2/K_1 should be equal to K.

It is noted that our empirical equation also resembles the one developed by Langmuir (1918) for the adsorption of gases on solid surface: viz.,

$$q = \frac{abc}{1 + bc}$$

in which q = amount of gas adsorbed per gram solid, c the equilibrium concentration and a and b are constants. Indeed, if we make the simple assumption that the rate of O_2-consumption (A), is proportional to the amount of O_2 adsorbed (q) on the respiring surface, the equation for adsorption may be considered applicable to this phase of respiration and a mechanism may be postulated for the mode of combination of O_2 with the respiring material on the basis of spatial arrangements of the molecules on solid surface as pictured by Langmuir (1918). This line of thought has to a certain extent been adopted by Freundlich and Fischer (1925), by Rideal and Wright (1925, 1926, *a*, *b*), by Quastel (1926), and by Shoup (1929–30). But since the question of the mode of combination of O_2 with the respiring material is far from being settled at present, it is perhaps wise for us to stop at the statement that the present equation expressing the rate of O_2-consumption in tissues and lower organisms as a function of O_2 tension is purely empirical, and until many more quantitative experiments are available pertaining to this question it is best not to attach too much significance to the constants of the equation. The mathematical identity of our equation with those derived for adsorption, dissociation, and reversible oxidation and reduction need not be taken as conclusive evidence supporting their physical identity. Among the recent accounts of the mechanism of oxidative catalysis in respiration may be mentioned those of Dixon (1930), Michaelis (1929), Elliott (1930), and Meyerhof (1924) and the literature cited in these papers.

It is noted that our treatment of the respiration data does not take into consideration the morphological aspect of the respiratory mechanisms such as those existing in fish and insects. It is assumed here that as long as the data secured with these organisms can be treated with the simple relation, as expressed by equation (1) or (2), it is immaterial to know, for our purposes, through what morphological channel the O_2 was made available. There are undoubtedly cases where morphological modifications of the respiratory mechanism occur as the O_2 tension is varied, and other factors as well as simple diffusion may come into play. In such cases, the data are not suitable for the kind of analysis used here. For this reason, it is desirable that future work dealing with the kinetics of cell-oxidation be performed on unicellular organisms. For a discussion of the morphological aspect of the respiratory mechanisms in the lower animals see Rogers (1927). A comprehensive morphological and ecological treatment of respiration in the fishes as related to O_2 tension is given by Powers *et al.* (1932). A similar account for insects is given by Wigglesworth (1931).

VI

We shall now treat equations (1) and (2) once more and attempt to analyze the behavior of the constants.

$$\frac{A}{A_0} = \frac{KP}{1 + KP} \quad \text{or} \quad A = \frac{A_0KP}{1 + KP}$$

Setting $1/A_0K = K_1$ and $A_0 = 1/K_2$, we have:

$$A = \frac{P}{K_1 + K_2P}$$

or

$$\frac{P}{A} = K_1 + K_2P$$

It is to be noted that when P/A is plotted against P, K_1, the intercept, corresponds to $1/A_0K$ and the slope K_2 is $1/A_0$. Since by experiment we know that $\frac{d\ln A_0}{dT} = \frac{\mu}{RT^2}$ (the Arrhenius equation) in which μ is a constant termed the "temperature characteristic" by Crozier (1924–25), K_2 should vary with temperature in such a way that when P/A is plotted against P, an increase in temperature will cause a decrease in the slope (K_2) of the line in the manner described by $\frac{d\ln A_0}{dT} = \frac{\mu}{RT^2}$. K_1, the intercept, contains the terms $1/A_0$ and $1/K$. While we know from above that K_1 is partially decreased by an increase in temperature because of the dependence of A_0 on temperature, the change of K_1 with temperature cannot be predicted without knowing the relation of the latter to K. The only experimental evidence on the change of K with temperature is that furnished by Warburg and Kubowitz (1929) with *Micrococcus candicans*. Their data for $\frac{n}{(1-n)P_{O_2}}$, (or K), ascertained for *Micrococcus* at 1°, 5°, and 10° are plotted on Fig. 3, together with the data for respiration at these temperatures. It is evident that K has a negative temperature coefficient ($\Delta H = -24{,}000$ cal.) while A_0 has a positive temperature coefficient of $\mu = 30{,}500$ cal. If we use the expression $\frac{d\ln K}{dT} = \frac{\Delta H}{RT^2}$ (which is van't Hoff's reaction isochore) as an approximation in describing the relation existing between K and T, we see that the decrease in K_1 caused by $\frac{d\ln A_0}{dT}$ will be more or less compensated by $\frac{-d\ln K}{dT}$, and K_1

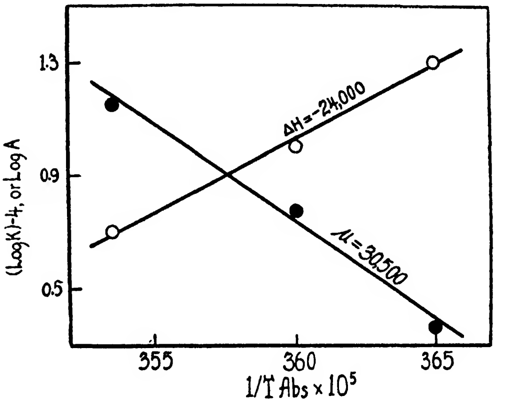

FIG. 3. LOG K $\left(\text{OR LOG } \frac{n}{(1-n)P_{O_2}}\right)$ AND LOG A (OR LOG Q_{O_2}) ARE PLOTTED AGAINST $1/T$

Data taken from Warburg and Kubowitz (1929) for *Micrococcus candicans*. The open circles are for the values of K, and the solid ones are for A. A, K, p_{O_2} and T are rate of respiration, equilibrium constant, O_2 tension in atmospheres, and the absolute temperature, respectively. $n = \frac{A}{A_0}$ in which A_0 is the rate of respiration in air (maximum rate). Since the points are taken at temperatures which are quite far apart, the slopes of the lines (μ) and (ΔH) should be considered only as approximations. The possible occurrence of a "break" in both curves at 5° (360×10^5 $1/T$) must be recognized.

should be more or less independent of temperature according to the relative magnitudes of μ and ΔH. While no comprehensive data whatsoever have been obtained which may throw light in this direction, it is interesting to compare the constants obtained with fertilized *Arbacia* eggs by Amberson and Tang and Gerard

(nos. 14 and 17 in Table 1). The data of the former were obtained at about 18° and those of the latter at 25°. It is evident from Table 1 that while the values of K_1 are almost the same in both cases (6.0 and 6.5) K_2 decreases from 0.95 at 18° to 0.55 at 25°. However, until much more comparable data are obtained, these calculations must be considered only as speculations.

In cases where the assumptions used for the derivation of equation (2) may be considered to be correct, and where K may be considered as the equilibrium constant of the oxidation and reduction of the intermediate substance *I*, then when K is known (either from K_2/K_1, or from equation (2)), the change in free energy as well as the redox potential for the reversible oxidation and reduction of the intermediate substance may be calculated by the relation (Lewis and Randall, 1923):

$$\Delta F^0 = -RT\ln K = -nFE^0$$

But since much has yet to be learned about *K*, such calculations must be postponed.

Whatever the theoretical interpretations of the constants may be, the formal relationships existing among *A*, *P*, and *T* may be described by the three equations:

(1) the equation of Warburg and others

$$A = \frac{P}{K_1 + K_2P}$$

or

$$A = \frac{A_0KP}{1 + KP};$$

(2) the Arrhenius equation, as adapted to biological processes by Crozier:

$$\frac{d\ln(1/K_2)}{dT} = \frac{d\ln A_0}{dT} = \frac{\mu}{RT^2};$$

(3) the reaction isochore of van't Hoff:

$$\frac{d\ln(K_2/K_1)}{dT} = \frac{d\ln K}{dT} = \frac{\Delta H}{RT^2}$$

When the constants K_1, K_2, μ and ΔH are known, *A* may be evaluated for any combination of *T* and *P* at which the three relations hold. Thus *A* is completely and quantitatively defined with regard to *T* and *P*, which in the simpler cases are the only variables of any consequence. Such a method of description differs from the "principle of limiting factors" of Blackman (1905) in that the latter is a qualitative statement of the change of a physiological process when one factor is varied at a time while the others are maintained at a maximum.

VII

To recapitulate: While the hyperbolic type of equation holds for the great majority of the data examined in this account, it is also true that data exist where the equation fails to hold strictly without undue modifications, as in the cases where the relation between oxygen tension and the rate of oxygen consumption is apparently linear. In such cases the relationship may be considered as being complicated by the presence of diffusion gradients in the tissues or in the media, or by the rate of circulation of the blood stream, etc., and it may merely be expressed empirically by $A = kP$. It is only in the last few years that attempts have been made to elucidate these factors, and mathematical expressions have been arrived at to approximate their relative rôles in respiration (*cf.* Shibata and Tamiya, 1930; Gerard, 1931; and Roughton, 1932). As yet none of these suffices to account for the available data in a quantitative way. At the same time the technic of measuring respiration has been greatly refined with the purpose of eliminating errors due to insufficient supply of O_2 to the respiring materials. In view of these recent developments, future work relating the rate of O_2-consumption and O_2 tension should be directed at sim-

plicity, and the materials and methods should be so selected that the number of uncontrollable and unknown variables be at a minimum. Where such rigorous requirements cannot be met, as in ecological studies, it is hoped that at least the results may be expressed in a readily intelligible and if possible, uniform manner, so that the constants, when ascertained under comparable conditions, may provide a basis for comparing the habits of different organisms.

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THE PROBLEM OF ACQUIRED PHYSIOLOGICAL IMMUNITY IN PLANTS (*Continued*)

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VII. ACQUIRED IMMUNITY IN PARASITISM

WE NOW come to the most interesting and practically most important aspect of the problem of acquired immunity, namely the acquired immunity displayed in nature. Abundant opportunities are offered in nature for sensitization. First and foremost one immediately recalls parasitism with its wealth of likelihood of the display of immunological phenomena. But no less interesting and instructive are the possible immunological phenomena attending the sensitization due to symbiosis of various sorts. We shall accordingly devote the present and following sections to a consideration of acquired immunity in parasitism and symbiosis respectively.

In order that the proof of acquired immunity be complete in these cases of natural sensitization it is necessary not only that immunological phenomena be observed *in vivo* (recovery from disease, resistance to superinfection, peculiarities of behavior of the foreign body within the host tissues, etc.), but also that it be demonstrated that such reactions are due to antibodies. This dual proof, the necessity for which has been well pointed out by Silberschmidt (161), has been resorted to in very few of the experiments and observations in this field, yet taken as a whole the evidence thus far available, as we shall see, renders very sound the hypothesis that reactions of the zoöimmunitary type do occur in plants and may play an important rôle in the preservation of plants in nature.

A. Immunity to reinfection

The most obvious manifestation of acquired immunity in parasitism is the complete or partial immunity of a host to reinfection after recovery from an earlier attack of a disease. Numerous observations of such immunity to reinfection have been made in the past twenty years and while all may not be due to acquired immunity in the zoöimmunitary sense, the evidence is certainly strongly suggestive of such in some cases at least.

First in point of time should be mentioned an observation of Smith and his colleagues Townsend and Brown in 1908 and 1909 (Smith, 1911: 162). These investigators obtained some evidence to show that after Paris daisies had been several times inoculated with *Bacterium tumefaciens* with the production of tumors, subsequent inoculations with cultures of the same organism were without effect. Later experimentation showed that this assumed increased resistance, however, was due, at least in part, to a loss of virulence on the part of the parasite. Smith likewise thought for a time that he had achieved resistance to the olive tubercle organism in plants which had been freely and repeatedly inoculated, but that too may have been due at least in part to loss of virulence of the parasite. In a second publication the same year (163) these workers

reported more extensive experiments with *Bacterium tumefaciens* on daisy in which the error due to loss of virulence was effectively eliminated in most of the experiments. Successive vegetative propagation and inoculation of Queen Alexandra daisy showed a decided refractoriness to infection after the third set of inoculations and vegetative propagation. This resistance was manifested in the extremely slow growth and small size of the galls. The virulence of the strains of bacteria was controlled in each case by the infection of fresh (never-infected) daisy or beet with the production of large, typical galls in a brief period. This work was continued by Brown in 1923 (27) when she reported that attempts to build up an acquired resistance of daisy and rose to the same parasite by repeated infections and vegetative propagation from such infected stock failed to show any permanent resistance, although a temporary acquired resistance was twice noted.

Arnaudi two years later (4) noted that the presence of a crown gall on geranium inhibited reinfection a few centimeters from the preëxisting tumor, and in 1928 the same worker published a further account of work with *Bacterium tumefaciens* (7) in which he found a somewhat greater susceptibility in geraniums which had never been infected than in plants with recent or old crown galls. Unfortunately Arnaudi's results were based on the reactions of only ten plants including controls, and since his difference between controls and experimental plants is not great one regrets that an accurate quantitative increase in resistance could not be accurately determined. Moreover, Nobécourt's experiments of the same type (136) failed to show any protective effect of preëxisting crown galls in *Pelargonium* and *Euphorbia*, a failure which Nobécourt believed might have been due to the distance between gall and inoculation. Finally a few additional experiments with this same organism were performed by Riker in 1926 (152). Riker inoculated with *Bacterium tumefaciens* plants both with and without galls but he failed to detect any difference in reactivity between the two types of plants. The possibility that antibodies had been produced but not circulated was rendered doubtful by his failure to find bacterial agglutinins, precipitins, or lysins in the gall extracts.

The only other experiments dealing with the effect of infection with bacteria on subsequent reinfection by the same bacterial species are those of Němec in 1929 (133) in which he observed an acquired immunity to *Bacillus pyocyaneus* (destructive by means of its toxins) in green varieties of cabbage, but not in blue varieties, and in *Crassula lactea*. Such acquired immunity was found to be somewhat restricted to the point of inoculation, however, and not freely circulated, although the inoculation of one side of the *Crassula* leaf offered a partial protection against the deleterious effects of subsequent inoculation of the other side of the same leaf.

Beside these experiments with increased immunity to reinfection by bacteria, observations of similar phenomena have been made regarding other types of plant disease. Thus in the case of fungus diseases of plants we have several such records. In 1911 and 1914 (170, 171) Tischler made some very interesting observations on the rust disease of *Euphorbia cyparissias* caused by *Uromyces pisi*. He found that it was possible to induce rapid and complete recovery from the rust attack by placing the affected plants in a saturated atmosphere at relatively high temperatures. Once such recovery took place the shoots were then no longer susceptible. Viable mycelium in the older portions of the plant was unable to infect the new growth and was even killed back. A similar effect was also accomplished by eliminating the win-

ter rest period of the host, in which case the mycelium remained viable in the vacuolated cells of the tips of the branches but was unable to penetrate the meristematic tissues of the vegetative point. Tischler interpreted these results in terms of nutritional and osmotic relationships between host and parasite, but it seems equally probable that his results are susceptible to an explanation in terms of an acquired physiological immunity. Further experiments *in vitro* would be necessary in order definitely to establish the truth of either of these hypotheses.

Montemartini in 1918 (121) observed that in that year the European oak suffered less than in preceding years from the mildew (*Oidium*). This decrease in the disease appeared to be due not to environmental conditions during that year but rather either to a diminished virulence of the fungus or to an acquired immunity of the host. Montemartini continued his observations for the following twelve years and by 1930 (122) was of the opinion that the disease was gradually becoming much less severe in general than in earlier years. Various hypotheses had been advanced to account for this decrease in the severity of the mildew, none of which had been supported by experimental proof. Montemartini accordingly performed a series of inoculation experiments in order to detect possible acquirement of immunity in parasitized trees. Twelve young oaks were used, of which six were protected from the disease in 1929 while the other six were permitted to become heavily infected. The following year all twelve trees were exposed to the disease. The six previously protected plants all showed heavy infection while the six previously exposed plants with one exception remained free from the disease.

A very similar type of observation was made in 1930 by Gravatt and Gill (70), who believed that the coppice growth from chestnuts killed by *Endothia parasitica* was annually becoming larger and stronger before succumbing to the bark disease. Just as in human disease so in plant disease one observes that all epidemics in time tend to become less and less severe. This waxing and waning of specific diseases is doubtless the resultant of many interwoven factors of which virulence of the parasite and susceptibility of the host are the most important. We have before us evidence that two such epidemics are now on the wane. In one case we also have evidence that this diminution in severity accompanies an acquirement of immunity in individual plants. Regarding the chestnut bark disease we have no experimental evidence to guide us, yet the sequence of events in the case of the oak mildew might afford a valuable clew to the understanding of the *Endothia* disease. Other epidemics are now threatening us: the devastating Dutch elm disease is at our door, the very destructive willow scab disease is sweeping down from the north and fast invading the northeastern states, the same is true of the beech canker disease and others. Sooner or later we must learn how successfully to combat these epidemics, and our experiences with the oak *Oidium* and the *Endothia* canker may have much to contribute to an understanding of the host-parasite relationship which must serve as the groundwork for our control of such epiphytotics.

We are indebted to Whetzel for a third observation of this same order (186), an observation which may best be related in Whetzel's own words:

> During my senior year in Wabash College I made some studies of the *Gymnosporangium macropus* which occurs very abundantly on cedars and apple trees about Crawfordsville, Indiana. I observed that certain cedar trees were very badly infected, being loaded with galls, large and small, on all their

twigs and branches. Other trees standing near were almost or quite free from any infection. A couple of years later I returned to Crawfordsville for a visit and went out again to see the cedar trees from which I had, during my senior year, gotten such large quantities of galls. To my astonishment they were practically free from infection, while others nearby that had borne no galls before were now badly covered with them. What the explanation of this phenomenon is I do not know. It occurred to me, however, that a serious infection of the trees one season might have rendered them more or less immune for a time. That the infection was on different trees in these two years is certain, as I was very familiar with the different trees with which I had worked.

Another observation of the same type concerns the *Hemileia* rust of coffee, as reported by Dowson in 1921 (56a). Dowson found that in East Africa the first attack of the rust disease is much more severe than subsequent attacks, from the standpoints of the number of rust pustules per leaf and of the number of leaves infected. This fact was interpreted by Dowson as indicative of an acquired immunity, since observations of adjacent plantations suffering from first and subsequent attacks of the disease showed that the virulence of the parasite remained constant.

Beside these more or less clear-cut cases of acquired immunity to fungus infection may be mentioned in passing the experiments of Doussain in 1925 (56). This worker found that if onions were infected with various molds, then crushed and mixed to form a paste and reinfected, the previously infected onions molded more quickly than those which had been not previously molded. This would seem to indicate a situation exactly contrary to that reported for oak *Oidium* and *Euphorbia* rust, i.e. a greater *susceptibility* following infection, but unfortunately Doussain's data are not sufficiently complete for one to draw suitable conclusions from his experiments. It may have been that the increased "susceptibility" shown was merely due to the presence of an abundance of mold spores from the earlier infection.

We have considered acquired immunity to reinfection in diseases caused by bacteria and by fungi. There yet remain two other important types of plant disease which have also been investigated in this connection, namely the diseases due to phanerogamic parasites and those due to viruses. Our evidence regarding the former is restricted to the findings of Heinricher regarding mistletoe infection of pear (71, 72). This investigator distinguished three relationships between pear and *Viscum album*, namely "true immunity," "true susceptibility," and "false immunity." The first two terms are self-explanatory. In the case of "false immunity" the pear shows an immunity to infection but not to the toxins of the parasite. Some of the "susceptible" plants were able to throw off the attack of the parasite and recover. Second and third infections were sometimes possible but lead only to very mild symptoms in the host as compared with the much more violent reactions of the host to the first attack. In many cases (97 per cent) reinfection was not possible after recovery from an attack of the parasite. This ability more successfully to withstand subsequent attacks was interpreted by Heinricher as being due to the acquirement by the host of "antitoxins" capable of neutralizing the toxins of the parasite, although he offered no further experimental proof of this hypothesis.

Finally, with regard to the virus diseases several investigators have contributed to a conception that plants recovering from such diseases do so through the agency of an acquired immunity. It is indisputable that plants suffering from virus diseases may recover in the sense that disease symptoms are no longer present; this has been amply demonstrated in the following cases: tobacco mosaic (Beijerinck, 1898: 11); *Abutilon* mosaic (Baur, 1906: Ber. Deut. Bot. Ges. 24: 416–428); tomato mosaic

(Brierley, 1915: 26); corn mosaic (Brandes, 1920: Jour. Agr. Res. 19: 517–522); sugar beet mosaic (Robbins, 1921: Phytopath. 11: 349–365); sugar cane mosaic (Kunkel, 1924: Hawaiian Sug. Cane Plant. Ass. Bull., Bot. Ser., 3: 115–167); sugar cane corn streak (Storey, 1926: So. African Jour. Sci. 23: 305–306); tomato mosaic (Verwoerd, 1929: 177); tobacco cucumber mosaic (Johnson, 1930: Kent. Agr. Exp. Sta. Bull. 306: 285–415); sugar cane mosaic (East, 1930/31: 60, 61, 62); cucumber mosaic (Porter, 1931: Iowa State Coll. Jour. Sci. 6: 95–129); tobacco virus diseases (Thung, 1931: 169a); and tobacco ringspot (Price, 1932: 142a).

But we must further indicate what is meant by "recovery." The problem in other words concerns the question whether plants no longer displaying symptoms still harbor the virus or not. If the virus is still present we may consider the disease as present but "masked" as in human pathology in the case of the typhoid "carrier." If the virus is no longer present we may consider the plant as showing *true recovery.* The literature as mentioned above contains examples of both masking and true recovery. From the standpoint of immunology both are of interest, since in both cases the freedom from symptoms may be attributable to an acquired immunity. In order to establish the proof of acquired immunity in such cases the experiments must include the following steps:

A. Are the "recovered" plants still infectious (masking) or not (true recovery)?

B. Whichever is the case, are the plants now immune to the virus originally used in infection (proof of acquired immunity)?

C. Are the plants still susceptible to other "species" of virus (specificity of the acquired reaction)?

All of these steps are desirable in proofs of the type before us. Let us see how thoroughly the experimental data serve to elucidate our theme.

1. With regard to the references cited above, in many cases cited the observations have not gone beyond the point of determining that plants have *recovered* from virus diseases. This applies to the works of Beijerinck, Brandes, Kunkel, Storey, and East.

2. Others have carried the matter one step farther; experiments have been performed to show whether the "recovery" was *masking* (true in the experiments of Robbins, Johnson, and Porter) or *true recovery* (true of the experiments of Brierley and Verwoerd). These workers, however, did not go on to the crucial experiments directly ahead, namely experiments to determine whether the plants were now immune.

3. Baur's plants showed *true recovery*, and reinfection with the same strain of virus originally employed showed them to be now immune. The specificity of this immunity was not investigated, however, and furthermore Baur's experiments are not considered very convincing. On the other hand, Price (Contr. Boyce Thomps. Inst. 4: 359–403. 1932) who was dealing with a case of *masking* found that the plants were now immune to reinfection with the same virus as originally employed, that the masked virus and the immunity continued through three vegetative generations with undiminished potency, and that immune substances were not transmitted from stock to scion through the graft union. Price did not test the reaction of his recovered plants toward other types of virus with a view to ascertaining the specificity of the immunity. Thung (Handel 6de Nederl. Ind. Natuurwetensch. Congr.: 450–463. 1932) who also observed complete recovery as well as masking found that plants diseased with one type of virus

were subsequently immune to a second "species" of virus. Birkeland (Phytopath. 23: 5. 1933) found no evidence of acquired immunity in tobacco mosaic and spot necrosis, but he was dealing with plants which showed neither recovery nor masking.

The evidence from the virus diseases is thus highly favorable to the theory of immunity acquirement in plants, and this is still further strengthened by Salaman's data on vaccination with viruses (Nature 131: 468–470. 1933) which show that infection of tobacco plants with an attenuate form of potato virus renders them specifically immune to later infection with a virulent form of the same virus. The facts as set forth are these: plants suffering from virus diseases may recover from their disease symptoms; in such "recovery" the virus may or may not still be present in the plants; whether or not virus is still present, such plants wherever tested have been found to be immune to further attacks by the same virus; this immunity has been shown to persist through three vegetative generations but not to be due to a freely circulated humoral substance: its persistence may well be due to the constant stimulation by the masked virus which is present. These data show that acquirement of immunity to virus diseases is a fact, and the last two points further indicate that the immunity thus acquired is closely bound up in the living cell, not freely diffusible, a point which will be stressed subsequently but one which in no way detracts from the thesis before us.

Accordingly we have before us a fairly significant body of data regarding increased resistance to reinfection after a first attack of a disease. These data afford answers, progressive if not complete, to certain important questions which confront us after a consideration of this subject. The first of these questions, namely whether or not a plant may show an increased resistance after one parasitic attack, would appear to have been answered in the affirmative. Several investigators have demonstrated such an acquired immunity after bacterial attack, fungus infection, and parasitism by a phanerogamous parasite. Although the number of investigations in this field is as yet limited it is significant that practically all are mutually confirmatory, and lead to the conclusion that plants may acquire an increased resistance after a primary attack of a specific disease.

Yet one must qualify these results and view them with a certain amount of caution. For in the first place few if any of these experiments considered alone are satisfactory proofs because of the failure to consider certain sources of error inherent in this type of experimentation. Thus in the first place all the investigations appear to indicate that the immunity to reinfection acquired by plants as the result of a first attack of a disease may be relatively weak, temporary, or localized. Accordingly particular emphasis must be laid on the detection of small but significant differences between control plants and experimental plants. This of course implies that both controls and experimental plants must be employed in sufficient quantity to make possible statistical studies. Experiments involving a few plants are of value in orientation, but the actual tests of acquired immunity should involve scores or hundreds of plants. Furthermore, since resistance and immunity are conditioned by a number of genetic and environmental factors, particular emphasis must be laid on the elimination of such normal variables. For example, that a plant is resistant to reinfection may mean that it has acquired immunity as the result of a first infection, but it may likewise mean that its greater

maturity at the time of the second attempt has increased its resistance, or that the environmental conditions surrounding the second attempt were not as favorable to infection as those attending the primary infection. One must therefore use a complete and extensive system of controls in order to eliminate errors due to such causes. Finally, in such experiments as this, one must conform to a complete schedule of proof just as in the proof of the causation of a parasitic disease one conforms to the postulates of Koch. In the present instance such a schedule should include:

1. A satisfactory primary infection shown to be due to the parasite in question.
2. Recovery from the primary infection.
3. Infection experiments to determine the susceptibility of such recovered plants at varying lengths of time after recovery and employing strains of the same pathogen of virulence equal to that of the strain causing the primary infection.
4. An adequate system of controls demonstrating that plants in every respect the same as the experimental plants except that they lack the primary infection are susceptible to the same parasite in a greater degree than the test plants at the time of the second infection.
5. In cases where there is likelihood of any doubt upon the question, the determination of whether the plants showing recovery have truly recovered or are merely harboring the parasite or infectious principle under such conditions as to produce no visible pathological symptoms. This particularly applies to a study of the virus diseases.
6. Determination of the degree of acquired immunity by the employment of some accurate mathematical measure; also determination of the duration, extension, and specificity of the acquired immunity.
7. A very valuable supplement to such experiments would be the comparison of the experimental results with observations of the disease in the field, as has been done in one case described above.

That immunity to reinfection may be acquired by plants appears evident from the experiments reported above, although more extensive and thorough experiments are needed to establish this point. That such acquired immunity may play an important part in the natural control of diseases in the field is likewise evident both from the theoretical relation of the experiments to plant pathology and from actual observations in the field such as those of Montemartini concerning oak mildew. As yet we have no adequate control of this phenomenon, but with the knowledge gained from such experiments as those described above we are equipped to carry into the field of practical phytopathology a new weapon of defense, biological prophylaxis. Before considering the part this may play in practice, however, it is first wise to discuss the experiments which have been performed dealing with the vaccination of plants, which will accordingly be the subject of the next few pages.

B. The vaccination of plants

We employ the borrowed term "vaccination" to include various methods of biological plant therapy. Vaccination in the medical sense implies the treatment of a subject with an attenuated strain of a parasite, the mild parasitism resulting conferring upon the subject an immunity to subsequent attacks of virulent strains of the same or related organisms. In the sense of the present paper, however, beside

this procedure others are included in the term vaccination. Thus the subject may be immunized subjectively (actively) by the introduction of an attenuated strain of a parasite, or objectively (passively) by the introduction of antibodies of either plant or animal origin. All of these methods have been attempted with plants, and will accordingly be successively considered.

First among the experiments in the *vaccination of plants with attenuated parasitic strains*, and indeed first in the field of acquired plant immunity, must be mentioned the findings of Ray (147) and Beauverie (10) in 1901. The contributions of these two investigators were so similar in many respects that they may be considered together. Beauverie in 1899 (9) reported that by the use of certain environmental variables (heat, cold, humidity, poor nutrition) he was able to vary the virulence of a sterile form of *Botrytis cinerea* ("toile") at will. In this way he was able to obtain strains of the "toile" which were sufficiently attenuated as to cause only a mild, temporary attack of the grey mold. Ray also accomplished the same end in 1901 (146) by the cultivation of *Botrytis cinerea*, a bacterium parasitizing legumes, and other parasites at high and low temperatures. Both workers then vaccinated susceptible plants with the attenuated strains thus obtained and observed the effect of this vaccination upon subsequent susceptibility. Beauverie immunized by planting *Begonia* in soil saturated with the attenuated *Botrytis*. The plants were not sensibly affected by such treatment. Subsequent transferal of such immunized plants to environments rich in virulent *B. cinerea* revealed that the plants resisted the parasite perfectly although non-vaccinated controls soon died from the effects of the virulent strain. Ray's experiments in vaccination are reported in much more detail than those of Beauverie and appear to be thorough and sound. Rigid attention was paid to such factors as sterility of soil and of seeds, purity of parasitic cultures, etc. The preventive inoculation was performed by injection of the plants at many points employing several preventive inoculations either with strains of equal attenuation or preferably with a series of strains of increasing virulence. The preventive inoculations resulted in slight infections from which the plants soon recovered, while the subsequent inoculations with virulent strains of parasites were wholly without effect.

For a long time these results of Ray and Beauverie remained unconfirmed, but during the past ten years several investigators have again taken up the same question. Brown's work with *Bacterium tumefaciens* on daisy and rose (27) has already been mentioned in another connection. Beside her findings regarding the resistance of galled plants to reinfection Miss Brown reported a few attempts in vaccination of these plants using dead bacteria as a vaccine. She found that vaccination of a point in the stem a short distance from a second inoculation one day later with virulent bacteria exerted no protective action against the second inoculation, but if the protective and virulent inoculations were made at the same point, only 20 per cent of the inoculations yielded galls as compared with 100 per cent in the first case. Miss Brown was not dogmatic in interpreting these experiments in the light of an antigen-antibody effect and wisely, because a double injection in the same point of a stem might well lead to errors due to the presence of inhibitory substances in the first inoculum. However, her failure to obtain protection at a short distance from the first inoculation is hardly conclusive evidence of the lack of biological protection because of the very short time

for antibody production and transportation (1 day) and her results in double inoculation of the same point are of interest in that they confirm the results of the investigations of Ray and Beauverie. Gheorghiu (67) has very recently performed an extensive set of experiments in vaccinating *Pelargonium* against crown gall using heated cultures of *Bact. tumefaciens* as vaccine. He obtained a strong specific protection and cure lasting three months.

Arnaudi has performed some experiments in this field during recent years working with a bacterium causing potato decay, *Bacillus mesentericus* (4, 6, 47). He attenuated the pathogen by ageing at 37°C and gradually adding lactic acid to broth cultures of the organism. This vaccine was applied to potato slices and subsequent inoculation of the virulent strain of the bacillus caused less severe and less rapid decay in the vaccinated potato slices as compared with the controls. Although his experimental tubers do not appear to be very numerous and although his results were not always very striking, yet his positive cases of decreased susceptibility after vaccination are sufficiently frequent to preclude the possibility of their being fortuitous, and Arnaudi's findings accordingly extend and substantiate those of the earlier workers.

The experiments of Beauverie with attenuated *Botrytis cinerea* have very recently been confirmed by Carbone and Kalajev (49a). These investigators also found that vaccination with the "toile" conferred an immunity on the host, although different techniques of vaccination yielded somewhat different results. The explanation of this discrepancy was found by Carbone and Kalajev to be due to a strict dependence of the acquired immunity upon a vital condition of the host. Injured or intoxicated hosts were less able to defeat the aggressive pathogen, and accordingly the vital character of acquired immunity in such vaccinated plants seems evident.

Vasudeva in 1930 (175) reported experiments in the double inoculation of apple fruits using successive inoculations of different organisms as well as inoculations with mixed cultures. In general he found that the presence of certain saprophytic fungi in association with certain parasites (as *Botrytis allii* in combination with *Monilia fructigena*) reduced the virulence of the parasitic attack. Vasudeva concerned himself with the question of whether the presence of the saprophyte resulted in an immunizing action upon the apple directed toward the parasitic fungus, and came to the conclusion that the decreased susceptibility shown could better be explained on the assumption of staling phenomena than by an immunological hypothesis. However, it does not appear from this work that there is sufficient ground for assuming that it either favors or argues against an immunological hypothesis. It is certainly difficult to conceive of the protective action of a "vaccine" of this sort administered at the same time as the virulent organism, and furthermore one would hardly expect that in any case vaccination with one species of fungus would cause an immunization against another very distantly related fungus. We have no analogy to such a situation in zoötherapy either in theory or in practice. Accordingly Vasudeva's results do not appear to afford any serious objection to the positive findings of other workers in this field.

In an unpublished lecture at Harvard University Dr. M. L. Rane mentioned work which he and others had done at the University of Chicago in the vaccination of plants (145). Taking advantage of the fact that "rough" bacterial strains are in general less virulent than "smooth" strains Rane and his associates performed

a few vaccination experiments but without success. Unfortunately the details of these experiments are not available as yet.

We thus see that a fairly comprehensive start toward a study of the vaccination of plants with attenuated forms of pathogens has yielded results which are very suggestive. Ray, Beauverie, Arnaudi, Brown and Carbone and Kalajev have all found that such vaccination resulted in a moderate increase in immunity. The available evidence of Rane's is as yet too incomplete to serve as a creditable objection to the findings of others, and moreover even though extensive negative results had been obtained, these would not serve to disprove the thesis, since in the problem at hand we have one in which, because of the exacting conditions of experimentation necessary to demonstrate positive findings positive results, if carefully controlled, are significant, while negative results are not necessarily so. Just as has been found in the display of acquired immunity following recovery and reinfection, so here in vaccination with attenuated pathogens we find that the degree of immunity conferred is not strong in all cases nor is it easily distributed through the plant, both of which again emphasize the need for complete and carefully controlled experiments in this field.

Vaccination with extracts of parasites is a second type of vaccination which has been attempted by a number of workers in the field of acquired plant immunity. Ray again inaugurated this type of investigation when he found in 1901 (147) that the water-soluble components of the alcoholic precipitate of virulent parasitic cultures if sprinkled upon the soil surrounding the roots of a susceptible plant confer upon that plant the same immune properties as if the plant in question had been subjected to infection by an attenuated strain of the parasite. Ray was not specific with regard to which particular host-parasite combinations he employed in this connection, but stated it as a general principle derived from observations of a number of host-parasite couples.

In 1925 Miss Zoja performed a similar experiment (192). She germinated seeds of *Triticum vulgare* in aqueous extracts of *Helminthosporium sativum* and of *Triticum* plants affected with this fungus and observed that after a few days the plants showed temporary signs of distress. Subsequent treatment with fresh *Helminthosporium* extract, however, resulted in no symptoms of disturbance, and when the plants were then exposed to potent *Helminthosporium sativum* they showed a complete immunity which lasted for at least one month. The active immune principle was found to be stable at temperatures below 50°–55°C. although it was destroyed by boiling. It appears from Miss Zoja's experiments, which were apparently carefully controlled and thoroughly executed, that she was dealing with a true case of acquired immunity induced by the antigenic functioning of the toxins or proteins present in the extracts.

During the same year Hursch (75) published an interesting account of experiments of this same general type. He cultivated parasitic fungi in liquid solution and then noted that such filtered solutions if administered to the host species produced in the latter symptoms of wilting resembling those of the parasitized hosts (as by *Fusarium*). However, plants so treated (e.g. cabbage and cauliflower) soon recovered when placed in fresh water, and if such plants were again placed in the same fungus filtrate they remained perfectly healthy, although untreated controls rapidly wilted in the fungus filtrates. There was a certain amount of individual variation among the plants in regard to their reaction to fungus filtrates which is

not to be remarked at since there is also much individual variation toward disease in the field. The nature of the toxic and antigenic components of the extracts was investigated and it was found that substances with various properties were responsible, although in general the severest symptoms were produced by those substances which were non-precipitable by alcohol, dialyzable, adsorbed by animal charcoal, and thermostable. They hence appear to be non-protein although apparently organic in nature and accordingly lend credence to the view that non-protein organic substances may in some cases be antigenic. On the whole Hursch's results appear to be significant, although details regarding his experimental procedures would be highly welcome.

The work of Sieden and Trieschmann reported in the following year (158) is of especial interest because it combines a theoretical study of acquired immunity resulting from treatment with parasite extracts with a practical application of such a procedure. These investigators worked with the serious potato wart disease caused by *Synchytrium endobioticum.* The first experiment in 1925 consisted in inoculating seed tubers with extract of overwintered warts by the use of a syringe. Such vaccinated potatoes, however, failed to show greater resistance than non-vaccinated controls. In 1926, on the other hand, the technique was varied in that the wart extract was introduced into bore-holes in the tubers which were then sealed again. The results of this second experiment were highly satisfying. In the fall the vaccinated potatoes had been attacked only slightly by the disease in a thoroughly infected field, while the controls showed numerous warts. Sieden and Trieschmann grant that as yet almost nothing is known regarding the comparative values of various techniques, but as their second experiment shows even these first tentative attempts have yielded results of significance in the economic struggle against the wart disease.

Arnaudi in 1928 (7, 47) performed some comparable experiments with a disease of *Pisum sativum* caused by *Blepharospora cambivora*. Pea seeds were germinated in (a) water, (b) extract of *Blepharospora*, (c) the same, but which had been heated to 60°, and (d) to 100°. The seeds in all cases but (b) continued to grow. When then inoculated with *Blepharospora* the vaccinated plants (c and d) were able to resist the attack and survive two weeks longer than the non-vaccinated controls, although eventually all were killed. The specificity of the vaccination was investigated in an exploratory way by vaccinating two lots of seedlings with *Aspergillus oryzae* and *Blepharospora cambivora* respectively. The seedlings were then all subjected to infection by *Blepharospora* with the result that the vaccination with *Aspergillus* afforded no protection against *Blepharospora* infection, the *Aspergillus*-treated plants behaving exactly as the non-vaccinated controls. It would hence appear that such vaccination affords a partial protection against subsequent infection, and the specificity of such protection from the scanty data available certainly suggests an analogy with animal vaccination.

In his monograph of 1928 (136) Nobécourt reports experiments of a similar type but using *Botrytis cinerea* and *Bacillus carotovorus*, both parasites of the bean. Sterile bean seedlings were watered with gradually increasing concentrations of extract of *Botrytis* cultures, a procedure which did not produce symptoms of suffering in the hosts. The infection experiments with *Botrytis* following this procedure demonstrated that the vaccinated plants showed complete immunity after 20 days, while the non-vaccinated controls were

severely decayed by the mold. Similar treatment of broad beans but using the filtrate of *Bacillus carotovorus* cultures produced an immunity of such a nature that the subsequently infected plants showed only mild symptoms followed by recovery when inoculated with the bacillus, while the controls showed rapid disintegration.

This type of experiment has been criticized by Hauptmann (49), who felt that plants so vaccinated were refractory to infection not because of acquired tissue immunity but because the tissues of the vaccinated plants were impregnated with the liquid of bacterial or fungus cultures and that increased resistance was due to the presence of this auto-toxic medium, i.e. containing staling products. Hauptmann's objection has been answered, however, by some convincing experiments of Carbone and Jarach (40, 44, 77). In this refutation *Phaseolus* and *Botrytis cinerea* were used as in Nobécourt's experiment reported just above. The bean seedlings were treated with *Botrytis* filtrate and subsequent infection showed that the vaccinated beans were more resistant to *Botrytis* infection than were the controls. Some of the resistant vaccinated plants were then killed by heating to 70°C, by ether vapor, and by cold (solid CO_2 at -45°C.). If the increased resistance of the vaccinated plants were due to the presence in the tissues of auto-toxic or staling substances, then the plants killed in this manner should be also resistant. If, on the other hand, the increased resistance were due to the vitally-associated antibody production, such killed plants should be quickly invaded and disintegrated by the fungus. The latter proved to be the case. The grey mold developed as strongly in the killed vaccinated plants as in the controls, and microtome sections showed an equal penetration of mycelium in both cases. We thus see that Hauptmann's objection is untenable, and, what is more interesting and relevant to the problem as a whole, that the acquired immunity displayed by the inoculated beans is a function of living tissues, alterable and lost at death. This affords a very strong analogy to the vital nature of animal antibodies and serves thus to strengthen significantly the case for true acquired immunity in plants.

There remains, however, one important objection to such vaccination experiments as the preceding which was offered by Leemann in 1932 (102). Leemann in studying the effect of various soil treatments upon the susceptibility of wheat seedlings to *Helminthosporium sativum* found that extracts and decoctions of various types of bacteria and certain fractions thereof in some cases increased and in other cases decreased the resistance of the wheat to the fungus. Among the treatments employed, Leemann found that a broth culture of dead and disintegrated *Helminthosporium* mycelium increased the resistance of the wheat, which fact if considered alone would serve as confirmatory of the experiments of the other workers reported above. Yet the protection against *Helminthosporium* afforded by extracts of *Bacillus fluorescens*, for example, indicates either that Leemann was dealing with a true antigen-antibody reaction which was highly non-specific, or that the problem of antibody production and demonstration in plants is complicated by the presence of other phenomena, perhaps analogous to staling. In other words, Hauptmann's objection, although not applicable to the *Phaseolus* experiments, may have an application when vaccination experiments as a whole are under consideration. An alternate but similar hypothesis is that the bacterial cultures may produce substances toxic not to themselves and thus not staling products in the customary sense but inhibitory to the development of *Hel-*

minthosporium much as Müller has found that certain inorganic fungicides and insecticides may be introduced into plants through the soil and play a part in the prophylaxis of plants (131). Leemann's work accordingly affords two important additions to our knowledge of vaccinotherapy, namely that in performing vaccination experiments we must take into consideration the possibility that the reactions may be due either to antigen-antibody effects or to the introduction of fungicidal or bacteriocidal substances in a simpler sense, another type of "pseudo-reaction," and second that in spite of this theoretical difficulty the practical application of vaccinotherapy is not interfered with but is perhaps aided, since the ultimate practical therapeutic value of vaccination is the same whether one or the other of these mechanisms is responsible.

Before leaving the subject of the active immunization of plants by vaccination we have yet to consider the experiments of Benigni regarding a slightly different aspect of acquired immunity. As was seen in an earlier part of this paper the peculiarities of plant disease may conceivably lead to different manifestations of immunity than are seen in animal immunology. As a representative difference between the two types of disease one may consider the rôle of the fungus spore in plant infections, a phenomenon having little analogy in animal immunity. Accordingly the experiments of Benigni on the effect of vaccination of *Zea mais* on the germination of *Ustilago zeae* spores are of particular interest. Miss Benigni in 1927 (12) germinated several varieties of corn seeds in water, Roulin's fluid, water and macerated smut spores, and Roulin's fluid and macerated smut spores. The seedlings in the smut extracts grew less luxuriantly than those in the pure liquids, but when later planted out these differences became less noticeable. Juices were then extracted from all four types of plant and smut spores permitted to germinate in hanging drops of such extracts. Germination was good in the plants which had absorbed only water, somewhat less in those which had absorbed Roulin's fluid, but almost *nil* in the plants which had been vaccinated. A little later, however, these differences were not apparent, and one may accordingly conclude that there is a certain grade of immunity in plants so treated expressed by an inhibition of germination of the spores of the parasite, although this immunity is partial and temporary, lasting, Miss Benigni believed, only as long as the pathological condition induced in the plant by the antigenic or toxic substances of the fungus. Leach, on the other hand, was unable to find in the extracts of rusted wheat plants substances which inhibited the germination of uredospores of *Puccinia graminis* (101).

Summarizing the results of the active immunization of plants by vaccination we may say that all of the numerous experiments thus far reported are in agreement in finding that such treatment of plants either with attenuated strains of parasite (Riker's findings excepted) or with extracts of parasite results in an increased and often very highly increased resistance of variable duration to the subsequent parasitic infection. As yet we know little about the precise nature of such prophylaxis. In some cases (Leemann) it appears to be due to a relatively simple absorption of fungicidal material. In other cases (Carbone and Jarach) it is bound to the living state of the protoplasm and is apparently of the zoöimmunitary type. The *fact* of acquired immunity by plant vaccination has been satisfactorily proved. Its *nature* awaits more critical study, but when one takes into consideration the other types of experimentation than vaccination, the

theory that acquired immunity of the zoöimmunitary type does occur extensively in the higher plants and plays an important rôle in natural prophylaxis appears to have been satisfactorily demonstrated.

Having considered the subject of the active immunization of plants by vaccination we have yet to note the very few experiments which have been performed in the *passive vaccination of plants*, i.e. in the introduction into plants not of antigenic material but of antibodies, either of plant or of animal origin. It is sometimes difficult from the nature of the experiment performed to determine whether a given experiment is illustrative of active or passive vaccination. Thus in the experiments of Sieden and Trieschmann (158), where the introduced substance was an extract of *Synchytrium* warts of potato, one is not sure whether the protection afforded was due to the antigenic stimulation of the *Synchytrium* substances (active) or to the antibodies of potato origin (passive). But there are a few cases which appear to illustrate that plants may be given successful therapeutic treatment by means of the introduction of antibodies.

Antibodies of plant origin were employed by Ray in 1901 (147), by Arnaudi in 1930 (47), and probably by Zoja in 1925 (192). The first investigator spoke of having successfully used preventive or curative antibody administrations to plants but gives us no details as to the exact nature of his experiments. Miss Zoja found that vaccination of wheat with extracts from diseased wheat plants served to inhibit later infection with *Helminthosporium*. This, however, may have been due either to an active or to a passive functioning of the vaccine as in the work of Sieden and Trieschmann. Arnaudi mentions only a single experiment of this nature in which the growth of a secondary tumor on geranium (*Bacterium tumefaciens*) was inhibited by joining to the place of the second infection a T-shaped tube of water leading to a primary gall. This evidence is accordingly very scanty and hardly serves to establish the point that antibodies of plant source may be used in the passive vaccination of plants.

In this connection should also be mentioned the experiments in which attempts have been made to vaccinate with antibodies of plant origin by means of grafting a susceptible with an immune plant. Wormald and Grubb (189) found that substances responsible for the immunity of apple to crown gall may be transmitted from immune scion to susceptible stock. In the cases of Chrysanthemum rust (Gibson, 68), the wart disease of potato (Roach, 153), and the downy mildew of potato (K. O. Müller, 130a) no such transmission of immunity-conditioning substances was observed. The experiments of Müller deserve a word of explanation because in these the basis of the work was definitely the conception of acquired antibodies in potato against *Phytophthora infestans*. Müller found that if susceptible varieties were grafted upon immune (wild) races of potatoes, and then infected, there was no alteration in the behavior of either susceptible scion or resistant stock, in the case where stock and scion were both infected more than three weeks after grafting (evidence against the circulation of normal antibodies), as well as in the case where resistant understock was heavily dosed with parasite inoculum after grafting but previous to the inoculation of the susceptible scion (evidence against the circulation of acquired antibodies). These negative results do not exclude the possibility of the activity of acquired antibodies in the cases mentioned, but resolve the question into three alternatives: (a) no antibodies are involved in the protective mechanisms under consideration; (b) antibodies are formed and passed from immune to susceptible graft·

partner but are chemically so changed in transit as to be rendered ineffective in protection; and (c) antibodies are elaborated but are not freely circulated through the plant. As will be seen subsequently, there is some evidence favoring the last of these three alternatives, but this question is assuredly worthy of more thorough investigation.

The only experiments involving the use of animal antibodies in plant therapy are those of Arnaudi (4, 6, 47) with crown gall of geranium. Arnaudi obtained a rabbit serum highly agglutinative to *Bacterium tumefaciens* and placed cut branches of geranium bearing galls in vessels containing weak solutions of such serum. After 10 days the galls in the anti-*tumefaciens* serum had withered up and shrunken while the control galls in water remained large and green. Moreover treatment with such serum followed by inoculation of fresh stems with *Bacterium tumefaciens* demonstrated a protective action of the serum against the formation of new tumors. Arnaudi's experiments involved very few plants, so few that one is not justified in drawing general conclusions from them. However, it is interesting to find that the few experiments which have been performed in the protection or cure of plants by means of the passive introduction of antibodies of either plant or animal source are all mutually confirmatory and we are thus oriented in and stimulated to investigate farther a field which from the practical standpoint of phytotherapy is no less significant than that of the active immunization of plants.

C. *The evidence from morphology and specialization in parasitism with particular reference to the cereal rusts*

The establishment of a parasitic relationship in plants is attended by a number of visible reactions on the part of both parasite and host. Such reactions, as for example the formation and appearance of haustoria, have long been described in plant disease but only recently have they been subjected to analysis in the light of their possible immunological significance. In animal disease a few such morphological reactions of immunological nature have been observed *in vivo*, e.g., the agglutination of bacteria, but the fact that in plant disease the fungus mycelium plays a predominant rôle leads one to wish to study plant disease in this connection in order to obtain evidence shedding light upon the other features of acquired plant immunity. Observations on the morphological reactivity of host and parasite in plant disease of probable immunological significance have now been reported by numerous investigators, and have been concerned both with diseases caused by fungi and diseases or infestations due to animal parasites, and accordingly these two phases will be successively considered.

As regards morphological disturbances of plant hosts and fungus parasites the first recognition of their immunological nature was due to Bernard in 1909 (17). In certain benign and localized plant maladies Bernard remarked that one often observes hypertrophy of cells with nuclear deformity, the nuclei in some cases even becoming amoeboid. At the same time the mycelium of the parasite is variously modified in the form of suckers or haustoria which may be globular, lobulate, or even ramified or arbuscular. According to Bernard these modifications are of immunological significance: the nuclei respond to fungus stimulation by becoming enlarged, amoeboid, and taking on a function similar to phagocytes in animal immunity. The gnarled or lobulate or otherwise deformed haustoria represent reactive forms of mycelium perhaps analogous to the agglutinated masses of bacteria *in vitro* in serology. Because of the necessarily artificial divisions of the present

paper it is necessary to anticipate slightly the next subject for discussion, immunity in symbiosis, to remark that Bernard's observations on parasitism were not the product solely of his work in this field but came more or less as a corollary to his more thorough work on symbiosis, which from Bernard's point of view is merely a specialized, controlled type of parasitism. His remarks on parasitic fungi apply particularly to the Uredinales and Peronosporales, in which highly specialized types of parasitism the morphological reactivity of the fungus mycelium is particularly evident.

In the invasion of cells by fungus haustoria an activity of the host is sometimes seen in the deposition on the haustoria of encrusting layers preliminary to a dissolution of the haustoria. This has been observed in the Peronosporales by Mangin (57), in *Blepharospora*, *Peronospora*, *Helminthosporium*, and *Alternaria* by Dufrenoy (57) and in *Peronospora* by Pantanelli (140). According to Pantanelli the membrane is a gluco-proteid analogous to chitin, while Dufrenoy finds it to be of cellulose.

Fischer and Gäumann (64) have pointed out the fact that in *Giberella saubinetii* infection of Gramineae the mycelium of the parasite is morphologically normal so long as it continues in the intercellular spaces of the host, but when it enters the cells the haustoria become deformed. Mueller (130) has also observed in *Hypochnus solani* a similar deformation, corrosion, and gradual dissolution of the older haustoria. These few examples will illustrate the type of phenomenon in which we are at present interested, although they are only representative of many other such observations.

Blackman in a general criticism of the theory of acquired physiological immunity as applied to plants (23) has recognized the reaction in infected plant cells, particularly in Erysiphaceae and Uredineae, which leads in some cases to the death and even to the digestion of the invading hyphae. This death and digestion of the haustoria, however, he interprets as being due merely to the lethal and autolytic processes attending the death of the parasitized cell, since "when susceptible forms are attacked we find no spontaneous cure, no recovery of the attacked cells."

Passing from the fungus diseases of plants to infestations by animal parasites we find additional evidence regarding the acquired morphological reactivity due to the stimulus of the parasitic relation. Bernard (17) has observed in melons invaded by the eelworm *Heterodera radicicola* the formation of giant cells with fragmented nuclei resembling phagocytes. Kostoff and Kendall (94) have also seen reactions in plants infested with nematodes, particularly displayed in the form of abnormal vacuolations, which they suppose may be regulated by the continuous immunological processes occurring in the affected parts which are stimulated by the toxins of the invader. This hypothesis is also employed by the same investigators to account for the structure and development of certain cynipid galls (93), where the galls are assumed to be formed in immunological reactivity to the antigenic stimulation of larval secretions, debris of injured cells, etc., to increase in size during the period of increasing but insufficient antibody production, and to cease development when the production of antibodies is sufficient for a neutralization of the antigenic material.

There thus appears to be no doubt that in many fungus infections and even in infestations of animal parasites the parasite and host cells exhibit profound morphological reactions to the parasitism.

How may these facts best be interpreted? It will be somewhat easier to answer this very difficult question a little later when we have considered the subjects of the restriction of the parasite in the host tissue and of symbiosis. At the present time, though, we find that the evidence offers some light upon the problem at hand. Let us consider the normal course of events in an infection such as that of the stem rust of wheat, *Puccinia graminis tritici*, as described by Miss Allen (1, 2) in infection experiments on several varieties of host.

The germination of the spores and penetration of the superficial layers of the host takes place in the same manner in both susceptible and immune suscepts. Once the fungus has penetrated, however, the resulting behavior depends upon the degree of susceptibility of the host. In a congenial host numerous haustoria are formed by the solution of a fine pore in the host cell wall through which the contents of the hyphal branch flow into the host cell. At this point the plasmatic membrane of the host cell is merely invaginated, not broken. The host cells are stimulated to increased metabolic activity and the nuclei increase in size several fold, but later they collapse. In a resistant host, on the contrary, a similar process ensues until a small haustorium is formed, at which time the host protoplasm, doubtless as a result of the toxic secretions of the haustorium, collapses and dies and becomes cut off from surrounding cells by thickened contact walls. Meanwhile substances formed in the host cell diffuse into the haustorium causing its collapse and death and even that of the hypha back of it for some distance. The relative speed of development of the haustorium and of death of the host protoplast vary considerably so that in some cases the host cell may be severely damaged at the time when the fungus is not visibly harmed, and in other cases the host cell may be still normal in appearance while the fungus has succumbed. Miss Marryat (120) has observed the same two types of reaction in resistant hosts. Miss Gibson (68) in an extensive series of rust inoculation experiments found that many rusts may penetrate wholly unnatural hosts, but that after penetration the fungi are killed, the conditions "seeming to suggest that the death of the entering hyphae is not due so much to starvation as to some poisonous substance emitted by the cells."

There are several possible hypotheses to account for the immunity and susceptibility of wheat to the stem rust. The hypothesis that the spores of the rust are not able to germinate or to penetrate the uncongenial host is invalid. Many investigators have observed equal or comparable penetration of the rust mycelium into susceptible and resistant hosts. The theory that the rust dies in a resistant host because of a lack of suitable nutriment is not supported by the behavior of the mycelium which unless it is actively killed back at cell after cell in its progress is able to derive some satisfactory nutriment from the host cells. The hypothesis that resistance is due to a pre-existent toxin or unfavorable environmental condition (e.g. osmotic relationships) present in the host cell also fails to conform to the experimental findings, for in many cases the fungus can develop rather extensively before it is ultimately killed, and moreover the very complex specificity of the cereal rust resistance, as will be treated of below, renders it inconceivable that a pre-existent and therefore presumably non-specific substance or condition could be responsible for the display of immunity. We are thus forced to consider a fourth hypothesis, namely that the immunity of the cereals to rust depends upon an active production of specific prophylactic substances within

the affected cells as a result of the specific stimulation of the fungus products. Such an hypothesis has much in its favor apart from the negative findings in the other possible interpretations.

In the first place the morphological behavior as recounted above leads one strongly to the impression that immunity here is dynamic and not static, active and not passive, chemical and not mechanical. The fungus penetrates the immune host. It establishes a small mycelium. Attempts at haustorium formation, however, are eventually thwarted and the fungus dies, but not in many cases until it has formed some functional haustoria. The injury of the host protoplast is assuredly due to the production of toxins by the parasite. Were such injury merely due to the progressive withdrawal of food from the attacked cells then there would be no subsequent death of the whole mycelium, although individual haustoria might die, but the mycelium as a whole would be expected to progress and gradually involve greater and greater areas of the affected leaf. Furthermore cells at some distance from the mycelium may be variously affected; stimulated to greater metabolic activity or even plasmolyzed. Moreover, where some germ tubes lie outside the host and others inside, the latter are killed much before the former, a condition not compatible with a starvation theory (68). Thus we are safe in concluding that the primary effect of the fungus upon the host cell is a toxic effect. What is the host's response to this? There are three possibilities. The host cell could passively succumb, it could neutralize such toxins by pre-existent prophylactic substances, or it could neutralize them by specific antibodies elicited at the time by the stimulation of the toxins. The first of these possibilities is rendered very doubtful by the fact that the haustoria are not only killed but that the adjacent hyphal stretches may be killed back for considerable distances and that all of this may happen before the host cells show any symptoms of distress. The second possibility, that of pre-existent toxins, has already been refuted above, its non-specificity and necessarily early action being inconsistent with the facts. The third possibility, that the mycelium is actively destroyed by new-formed antibodies is, on the other hand, perfectly consistent with the morphological behavior of host cells and haustoria. The haustoria may penetrate, may derive some sustenance from the host cells and not until time has elapsed for the host cells to react by immunological mechanisms do death and disintegration of the haustoria ensue. This time may be of varying duration. In some cases it is very brief and the haustorium is killed before it is very well developed, in other cases it is fully expanded before the acquired lethal effects of the host cell become evident (the mycelium in such cases occupying broad expanses of the leaf and perhaps attaining to one stage of fructification before it is ultimately killed), and in still other cases the host cell is so tardy in its production of antibodies that the protoplast dies from the toxic effects of the fungus without succeeding in exerting its direct antibody effect upon the latter, which is, however, killed indirectly due to the loss of food in the dying cell or to the autotoxic effects of the dying protoplast, or to both. In all cases, however, the haustorium dies, and the reaction is sometimes sufficiently great to be communicated back along the mycelium, resulting in death of the adjacent hyphae. Such a sequence of events is in full accord with the morphological picture in rust parasitism and serves to explain the facts as no other assumption does. But there is further evidence for

this immunological interpretation of the cereal rust resistance.

The second line of argument for the hypothesis of acquired immunity in the cereal rusts is that of host specialization, a subject which has been well treated by Fischer and Gäumann (64). The complexity of specificity in the rust diseases of plants as well as in the diseases caused by other types of parasites has long baffled students of plant immunity. There are approximately fifty biological races of *Puccinia graminis tritici* distinguished by their differential aggressiveness toward a dozen or more races of *Triticum*. There is no correlation between immunity in one host-rust combination and immunity in other such combinations in the case of wheat stem rust. A given race of the rust may attack all varieties but one or two of the wheat, or it may attack relatively few, and the variety of wheat which is immune to any given strain of the rust may be susceptible to any other given rust race. The situation is so complicated that it is wholly impossible to explain it on the basis of the assumption of simple pre-existent toxins or unfavorable environmental conditions without postulating an enormous number of such substances and an equally large number of variable physiological properties in the fungi for combatting them. It is equally impossible to explain the complexity of wheat stem rust on the basis of mechanical features. But when we analyze the problem in the light of acquired immunity in combination, perhaps, with other simpler immunological mechanisms, the problem becomes somewhat clearer. Acquired immunity in animals is characterized by its complex specificity, a specificity so complex in fact that immunological reactions afford the only precise general technique for distinguishing individual proteins from one another, and the assumption of such reactions underlying the immunity display in the cereal rusts would afford an explanation and indeed the only conceivable explanation of its complexity.

Thus far we have considered the complexity of the specialization of varieties of a given host species toward strains of a given species of parasite. But the problem of host-parasite specialization is still more involved when one considers that thousands of species of parasites are restricted to a given living host species or variety, although they may be artificially cultivated upon the most diverse dead media. There is plainly some function of the living protoplasm of resistant species which prevents the development of the parasite and which is lost at death. This is further demonstrated by the facts that narcotized plants are often more susceptible to infection than before narcosis, as has been shown by Reed and Cooley with the *Heterosporium* disease of spinach (149), by Stakman with wheat rust (166), and by Bolle with the *Alternaria* disease of *Brassica* (24), and that if immune hosts be killed in such a way as to alter least their chemical properties (e.g. by formaldehyde vapor) they may be rendered favorable substrata for growth of their parasites as has been observed in lupin by Fischer and Gäumann (64), and that in such diseases as the downy mildew of potato there is a distinct correlation between metabolic activity of the host and its degree of immunity, although in the meristematic tissues the mechanical defences are weakest (K. O. Müller, 130a).

Returning now to the specific case before us, that of the wheat stem rust, we are in a position to formulate a working hypothesis as to the exact processes involved under the various conditions of immunity. The young mycelium penetrates the cells as haustorial primordia. These secrete specific antigenic substances,

toxins or proteins, which simultaneously injure the host protoplast and stimulate that protoplast to the formation of specific antibodies directed toward the fungus products in question. Such antibodies are in the form of antitoxins, neutralizing the toxins secreted by the fungus, in the form of "agglutinins" which cause a deformity of the haustoria, or in the form of lysins, disintegrating the haustoria. Any combination of these may be present. The length of time necessary for the active functioning of the host antibodies conditions the extent of parasitic development before the death of the mycelium. Meanwhile the fungus itself may be active in counter-prophylaxis, fighting the effects of the destructive host secretions by its own elaborated system of protective bodies. Here as in animals there would be a resultant of these two counter processes which would determine the success or failure of parasitism. The production of specific neutralizing substances depends upon inherited potentialities in this direction which would condition the occurrence and efficacy of antibody production. Successful parasitism would then depend upon many steps and would be the resultant of numerous conflicting forces within the plant. It would require successful penetration of the mechanical barriers of the host, ability to live in the inner environment of the host by tolerance of its normal internal conditions of acidity, osmotic pressure, etc., ability to counteract inhibitory substances either normally present or produced as a result of parasitic stimulation, and capability of utilizing the food supplies available in the host. The hosts may vary in all these characters just as do the parasites in their ability to defeat the various host defenses. Any or all of these defenses and reactions to defense may condition a given case of parasitism, and successful parasitism must be understood as a final product of many such interacting factors. In the case of rust resistance before us the evidence points to the fact that the greatest stress in the host's defense must be laid on the acquired ability to counteract the fungus secretions and at the same time to injure the invader by toxic or lethal host secretions, but one must still bear in mind that the complex situation of the wheat rust specialization is doubtless the product of other defenses operating in a supplementary way in conjunction with the acquired prophylaxis.

These findings in the example chosen of wheat rust doubtless apply broadly throughout the field of phytopathology. Similar morphological reactions and similar, if not as well understood, host-parasite specializations occur in many other types of disease, and although it is not possible at the present time to extend this analysis to other cases of parasitism it is to be hoped that the results of the analysis of this case may find a broader application in the understanding of the nature and rôle of immunity in plant disease in general.

One point which it would be well to consider in this connection, however, is the fundamental reason for the narrow host restriction of many parasitic species. Fungi vary enormously in their host ranges from such types as *Phytophthora cactorum* which can parasitize plants in many widely diverse families to such as the rusts which are often restricted to a single species or variety of host. Yet in the rusts many may parasitize only two species of host but these two species may be widely removed systematically from each other, as for example conifers and ferns (*Milesia*) or conifers and composites (*Coleosporium*). Surely this type of specialization cannot depend upon a condition such that only one type of suitable nutri-

tion exists for the parasite in question and that that is found only in two such widely diverse hosts. Or can the fact that such a narrowly restricted parasite as *Phytophthora syringae* (parasitizing only lilac) grows on a very wide variety of dead substrata be reconciled with the belief that only in lilac is there to be found suitable food? And that immune plants killed by formalin vapor or anaesthetized with ether or chloroform become susceptible, does this indicate a lack of suitable nutrient in the active host? On the contrary these observations all lead one to the conclusion that immunity on the whole is not due to the lack in immune species of products which can be employed by the parasite as food but to the almost universal presence in plants of substances or conditions inimical to parasitism by all but a very few species of parasites. Such defenses may at times be mechanical, they may be chemical and congenital, but when one considers the many instances on record in which reduction of the vitality of the host makes possible a parasitism we are very strongly led to the conviction that a major rôle in plant defense is played by mechanisms which are directly dependent upon the vitality of the host, the mechanisms which we are here considering under the term of acquired physiological immunity.

We may summarize the findings of the present section before proceeding to the next subject for discussion. It has been shown that in many cases of parasitism both the fungus and the host react by pronounced morphological or cytological changes. On the part of the host such changes take the form of modification of the nuclei and plastids, vacuolation, hypertrophy of the cell, stimulation to increased metabolic activity, gall formation, etc. On the part of the fungus parasite such changes are chiefly manifested by the formation of modified branches or haustoria within the infected cells. The changes in the host may be chiefly non-immunological, due to its altered metabolism. The changes in the parasite, on the other hand, are probably often of immunological significance. The attack of the host cell upon the invading mycelium may be due to substances or capabilities congenitally present in the host, such as the ability to attack the mycelium by means of phagocytosis, to encrust the haustoria, etc., or to substances elicited by the stimulation of the parasite, i.e. antibodies. One must be very cautious in drawing the line between these two types of host reaction, since it is not unlikely that certain of the host reactions described as due to an acquired immunity of the host are in reality congenital.

In the case of the stem rust of wheat which is treated in detail it seems very plain that immunity here depends in large part upon defensive reactions of the host acquired as a result of stimulation by the parasite. Moreover, extension of the analysis of wheat stem rust to a broader consideration of parasitism of plants in general leads one to the conviction derived from several types of investigation that acquired physiological immunity plays a major rôle in the phenomena of plant disease immunity and host-specialization.

D. Limited growth or death of the parasite within the host tissues

It frequently happens in pathology that a satisfactory state of parasitism may be attained but that sooner or later the development and activity of the parasite are checked so that infection spreads no farther and the plant may recover. We find this particularly true, for example, in many of the leaf spot diseases of plants,

where a given fungus causes spots of an approximately characteristic size but appears to be checked in attempts to continue mycelial development beyond certain limits. In some cases such phenomena may be due to normal causes such as the restriction attending maturity of a tissue which is susceptible only when tender and succulent. In many cases, however, such restriction appears to partake of the nature of an acquired immunity, and it will accordingly be the purpose of the present section to discuss such cases.

In bacterial infections of plants Schiff-Giorgini (155) and Carbone (36) have both observed restriction or death of the parasite after a satisfactory commencement to infection. The former investigator found that in the bacterial tubercle disease of the olive the parasitized plant develops a thermolabile lethal substance as the result of stimulation by the bacteria, which, in connection with other means of defense, serves to localize the infection. Carbone also found a similar condition in potatoes infected with bacteria, where the bacterial infections were sharply delimited so that further development did not occur.

In fungus diseases of plants we have the experiences of several workers to support the same thesis. Tisdale in 1917 (172) found that both susceptible and resistant flax plants may harbor the wilt fungus, *Fusarium lini*, but while in the susceptible plants the fungus freely develops, in resistant plants it seems to be less vigorous and abnormal in its staining reactions. There are formed in resistant hosts modified corky walls which serve as mechanical barriers to the further progress of the parasite, but it is the opinion of Tisdale that these would fail to afford protection were it not that the fungus is. weakened by some toxic or other chemical substance produced by the host.

Kunkel in 1918 (99) brought out a most interesting condition in cabbage club-root caused by *Plasmodiophora brassicae*. He found that with striking consistency approximately 28 unit volumes of the "clubs" are occupied by the parasite in every 100 unit volumes of tissue.

> Each club is as thoroughly diseased as is possible. The non-infected cells are apparently free of infection not because they have accidentally escaped but because of some influence which the host exercises over the parasite. There is a limit beyond which the parasite cannot go in its growth in the cabbage tissues. How this limit is maintained is a problem that remains to be solved. It may be that the spread and growth of the parasite is held in check through the development of some protective substance in the host cells. The infected cells seem to have some means of controlling the growth of the plasmodia which they contain. If we assume that this control is exercised through the production of a protective substance or antitoxin, then it is easy to suppose that this substance might diffuse out into the surrounding cells and thus render them immune to attack. Before the parasite would be able to establish itself again in a cell it would be necessary for it to pass beyond the region of immune cells (l. c. pp. 566, 567).

Moreover in rare instances Kunkel found that almost all of the cells of a club may show infection, but in such cases the plasmodia remain very small and fail to stimulate the host cells to abnormal growth. This affords a very clear indication of the active rôle played by the host in restricting the advance of the parasite as a result of stimulation by the parasite.

Dufrenoy in his studies of diseases caused by a number of types of fungi (*Chrysomyxa*, *Blepharospora*, *Colletotrichum*, *Phytophthora*) (57, 58) found that resistance to these is a phenomenon manifested by a restriction of the mycelium after it has established a nutritional relationship with the host. This restriction results in the production of small, localized lesions, and Dufrenoy finds that the restriction is accompanied by the rapid formation of

phenolic compounds at the margins of the lesions. In the downy mildew of the vine Pantanelli (140) reports that the mycelium is restricted to the intercellular spaces, and where in exceptional cases branches are sent into the cells, these are rendered non-functional by an active defense reaction of the host.

The male gametophytes and embryos of flowering plants are parasitic. The growth of the pollen tube through the stylar tissue, for example, is closely comparable with the growth of fungus mycelium in plants. It is not surprising, therefore, that observations made on pollen-tube growth and embryo development should have led certain workers to immunological conclusions with regard to this process. Ward in 1902 (183) was the first to call attention to the possible immunological behavior of maternal tissue toward the male gametophyte when he suggested that immunity of *Bromus* to *Puccinia dispersa*, a phenomenon which he believed due to specific antitoxins (184), was resembled by the factors governing fertility and sterility of the stigma to pollen. East (59, 60) and Kostoff and Kendall (88, 93) in 1929–1931 have further developed this same concept. East suggested that the secretions of a growing pollen tube may act as antigens toward the stylar tissue, which latter in developing antibodies toward the pollen tube would inhibit the development of the tube. This process would aid in explaining the sterility of stigmas to distantly related pollen (which would be more diverse antigenically than more closely related pollen) and although speculative this serves as a possible explanation of the behavior of the pollen tube within the maternal tissues. Kostoff and Kendall observed that the crossing of very distantly related species and very closely related genera often produces hybrid embryos, but these embryos die very early in development, which according to Kostoff's unpublished investigations was attributed to immunological causes.

We thus have a fairly extensive body of data dealing with the activity of plant hosts in restricting or killing their invading parasites. As yet all of the evidence available is based upon observations, no one case having been subjected to critical experimentation. We must accordingly be cautious in evaluating these data. The numerous completely confirmatory observations and the complete lack of contradictory data, however, strike one as being very suggestive, and *a priori* reasoning certainly renders it very doubtful whether any other hypothesis than an immunological one could explain the facts. We know, for example, that in all these cases the parasite first establishes itself and for a period of varying duration is successful in its parasitism. We know that ultimately this state is interrupted. The parasite begins to show symptoms of injury; it grows no farther or even dies. It is obvious that this is due to some property now present in the host but absent previously: it has been acquired. We also know that there is no evidence that the acquired capacity for restriction of the parasite is morphologically or cytologically demonstrable. We therefore assume that it is chemical. Being chemical it may or may not be of the antibody type, but it is rather difficult from our knowledge of immunity to imagine it otherwise than immunological. Careful and ingenious experiments are necessary to prove its nature. These may be impossible at the present time because of the inherently vital nature of the processes under consideration. All we can say is that the acquired immunological interpretation of these phenomena does serve to afford a satisfactory explanation of

them. No other hypothesis yet advanced serves to explain them so satisfactorily.

Before passing on to the study of the serological experiments in parasitism it is well for the sake of completeness and to avoid confusion to mention briefly another very interesting aspect of acquired immunity in parasitism which results when one considers the behavior of the rust fungi toward highly immune hosts. We find (Stakman, 166; Zimmerman, 190; and others) that there are three distinct categories of behavior of suscepts toward rusts. The rust may penetrate and successfully parasitize, a condition of susceptibility; the rust may penetrate but because of its inability to withstand the defensive reactions of the host it may perish, a condition designated as immunity; and finally the rust may establish a highly successful parasitism on a small scale toward which the host is unable to react in a defensive fashion, resulting in the rapid killing of the first cells invaded. But in this last case the death of the infected cells before the mycelium has been able to spread widely through the tissues means the sudden withdrawal of a source of nutriment to the fungus since only living protoplasm may serve in this capacity. The fungus accordingly dies, and the infection is recognizable in the leaf only as a small dead area which spreads no farther. This last type of reaction has been designated by Stakman as "hypersensitiveness." Practically its result is an immunity of the plant. Actually this "immunity" is the result of a *susceptibility* too great to make possible the parasitic relationship. As in the case of the symbioses to be considered later, a successful continuation of the relationship between vascular plant and fungus is possible only when the host is sufficiently susceptible to permit establishment of a nutritive mycelium and sufficiently resistant to prevent that mycelium from destroying the host. Here we have an apparent paradox. Acquired immunity in animals results in the removal from activity of injurious bodies. In plants the same is doubtless in general true, but in the case of the rust diseases (and in symbiosis, which is a controlled parasitism) a certain degree of acquired immunity is indispensible to successful parasitism.

This phenomenon was noted by Stakman and subsequent investigators of the cereal rusts. Mr. I. H. Crowell in an extended series of infection experiments with *Gymnosporangium* informs me that here too he has found that one often observes infection followed by death of the infected tissues with no subsequent spread of the fungus. I have also repeatedly observed it in aster species which exhibit a differential susceptibility toward *Puccinia asteris*. In the most resistant species which are attacked the infections of the fungus are represented by very small areas which are at first yellow but very shortly die. In less resistant species, however, the primary infection may attain a diameter of several millimeters and may even form functional aecia before dying. In the same way according to Crowell some species of *Malus* are so resistant that the infections become no larger than pinheads, others permit the spots to prosper to a stage in which they produce pycnia but then die, while in still others the infections may even produce aecia before succumbing.

Although this phenomenon of hypersensitiveness is closely simulative of the parasitic restriction described in the earlier part of this section, it must be differentiated from the latter because of its entirely different causation. The one appears to be a true case of acquired immunity, the other is quite the reverse. One very important aspect of the distinc-

tion of these two types of fungus localization is brought out in attempts to determine the susceptibility of host species to a given rust. In such attempts a clear distinction must be made between hypersensitiveness and partial or restrictive immunity, because theoretically they are diametrically opposed, and because practically attempts at breeding for resistance might not succeed if one fails to consider that a potential parent species may be immune either because of a strong defensive ability or because of such great susceptibility that the fungus cannot survive within its rapidly dying tissues.

E. *Acquired serological reactions in parasitism*

Acquired immunity in parasitism may be displayed in a number of ways. We have already considered several of these, namely immunity to reinfection, effect of vaccination, morphological changes, and restriction or death of the parasite within the host tissues. While it has been possible from a consideration of the evidence from these sources to establish the conception of acquired immunity in parasitism with comparative certainty, the final, and from the zoöimmunitary point of view the most important type of evidence is that yielded by serological tests. A complete proof of such acquired immunity requires evidence of increased resistance *in vivo* which is proven by serological tests to be due to antibodies. In animals this dual proof is a comparatively easy matter, but the reverse is true of plants. We have already seen the great difficulties besetting a serological study of plant materials. Nevertheless a number of experiments in this field have been performed and their results are of interest in concluding our discussion of acquired immunity in parasitism.

The first tests of this nature were performed by Schiff-Giorgini in 1905 (155) working with the olive tubercle disease. Pieces of wood from points near an infection were dropped into bouillon cultures of *Bacillus oleae* and led to agglutination and lysis of the bacteria, while control tubes remained unchanged. This production of protective substances was apparently localized about the lesions and did not confer an immunity on the plant as a whole, since each year the number of tubercles increased.

Mention has been made of Leach's experiments in 1919 (101) in which he was unable to demonstrate in juices of rusted wheat plants substances inimical to the germination of rust spores. This is not a situation strictly comparable to animal serological reactions, however. Such a type of reaction might be immunological in plants but the absence of inhibition of spore germination does not imply absence of any immunological control in such cases. Indeed we have already seen that in the cereal rusts acquired immunity is not expressed until long after the spores have germinated and then only within the living cell. Leach's results are accordingly of interest but they do not seriously handicap the acquired immunological interpretation of wheat rust resistance.

In 1923 Carbone performed some experiments in the demonstration of agglutinins and lysins in potato decays caused by several species of bacteria (36). After having introduced the bacteria into potato cavities for several days he expressed the sap from portions of the tubers and tested this sap against suspensions of the bacteria but with wholly negative results in every case. Carbone's experiments were carefully controlled and his tests were performed with strict adherence to the approved methods of animal serology. The argument that potato tubers are quiescent organs and lack the activity of green

tissues was refuted by Carbone's observation of the rapid and active cicatrization of the potato wounds, but he felt that possible failure in absorption of antigenic material might have accounted for his negative findings.

The following year Kořínek (81) continued this type of investigation using as experimental material crown gall of *Beta* (caused by *Bacterium tumefaciens*) and bacterial infections of *Euphorbia* and of Leguminosae. With the legumes and beets a technique similar to that of Carbone's was used, but with *Euphorbia* the latex was tested for its antibody content. The inoculated beet sap strongly agglutinated *Bacterium tumefaciens* but equally agglutinated *B. prodigiosus*, and the non-inoculated controls also showed strong normal agglutination. Accordingly his results with beets are not to be considered of immunological significance because of the error due to the strong normal agglutinins. The agglutination observed was therefore termed a "pseudo-agglutination" both because of its non-specificity and because microscopic sections showed it to be doubtless due to a chemotactic action of crystals present in the root sap. The *Euphorbia* latex, on the other hand, was found to contain neither normal nor acquired agglutinins toward inoculated bacteria of several species, and the same was likewise true of various inoculated species of legumes. Kořínek's evidence is accordingly wholly negative. What "antibodies" were found proved to be non-immunological in their causation and behavior.

Sardiña in 1926 (154) performed some carefully controlled and executed experiments for the demonstration of antibodies in a number of types of plant infections. In the case of *Opuntia* infected with the potato blackleg bacterium the inoculated plants showed acquired precipitins while the non-inoculated controls were negative, but in all other cases (*Opuntia*, *Lycopersicum*, *Cucurbita*, *Solanum*, with several species of bacteria) acquired precipitins and lysins were not found. Sardiña was accordingly led by his negative results to the conclusion that species-specific agglutinins and precipitins are not formed in these species and that in this respect plants differ from animals and man. Technically Sardiña's work gives every evidence of care and thoroughness and may be regarded as a satisfactory demonstration of the results obtainable by the expressed-sap method.

Negative results were also obtained by Riker in 1926 (152) using the same technique. The expressed sap of plants bearing crown galls was found to exert no agglutinating, precipitating, or lytic action upon suspensions of *Bacterium tumefaciens*. That antibodies might have been produced in the galls but not circulated was apparently argued against by the fact that the bacteria grew as well in the expressed sap from the galls as in the expressed sap of non-infected controls. Riker accordingly came to the conclusion that either antibodies are not produced in crown-gall or else they are in insufficient quantities to be measured by ordinary methods.

To the experiments reported above should be added mention of East's experiments with sugar cane mosaic in 1931 (61). East found in a series of "precipitin tests" of expressed sap of various types of sugar cane that there is some indication of a consistent reaction difference between cane which has never had the disease and cane which has or may have had the disease. This evidence, though acknowledged by East to be very slight, appeared at the time to be serological evidence supporting the thesis that sugar cane recovers from mosaic by an immunological process.

Beside these serological tests of diseased

plants one must also make mention of the serological interpretations advanced by certain authors to explain the reactions of plants to infection. Thus, for example, Heinricher felt that the acquired resistance of pear to mistletoe could only be explained on the assumption of a toxin-antitoxin reaction (71, 72), Steiner considered that the specialization of the nematode diseases of plants is explainable by the same hypothesis (167), and Kostoff and Kendall also advance a serological theory to account for the reactions of Solanaceae to nematode infestations (94).

We thus see that the problem of the demonstration of acquired immunity in plants by serological techniques has been attacked by numerous workers. Their experimental results may be grouped into three categories: (a) demonstration of non-immunological pseudo-antibodies (East, Kořínek); (b) demonstration of no acquired serological reactions (Leach, Carbone, Kořínek, Sardiña, Riker); and (c) apparent demonstration of the acquirement of antibodies (Schiff-Giorgini).

Regarding the first class of reactions Kořínek has shown that his positive results are not only non-specific but that they are due to a simple physico-chemical mechanism, chemotaxis. East's technique has since been studied by Chester and Whitaker (52, 53) and although the results at first are strongly suggestive of an immunological character, the analysis of these latter investigators has shown that the "precipitin reaction" technique of Kostoff, East, and others is in no case observed immunological, but that the reactions observed are interpretable in the terms of simpler non-immunological chemistry.

As concerns the second group of experiments, it would seem that the technique of testing of the expressed sap against pathogenic bacteria has been satisfactorily demonstrated to reveal no antibodies. We have the evidence of five careful experimenters all mutually confirmatory in finding that the expressed sap of the infected tissue fails to exert immunological action upon the parasite involved. Against the results of these investigators those of Schiff-Giorgini stand in isolated opposition, alone and unconfirmed. The evidence of Schiff-Giorgini can accordingly be given little weight in comparison with that of the other investigators. Either his technique or material were more favorable in some unrecognized manner, perhaps due to the fact that he used pieces of infected tissue and not expressed sap for the source of antibodies, or else he was dealing with reactions of a "pseudo" or normal type, and it seems likely from the thoroughness of the subsequent experiments that the latter of these suppositions is the correct one.

If then we are to conclude that all of the serological tests in parasitism are either non-immunological or negative we are confronted by a paradox demanding explanation, for certainly the numerous observations *in vivo* point definitely to an acquired immunity in parasitism. How may this apparent paradox be explained?

There are certain marked differences between the techniques of animal serology and those which have thus far been employed in plant work. Chief among these is the very considerable change which must occur in the expression of sap from living cells. It has already been shown in several instances that acquired immunity in plant parasitism is a function of the *living cell*. Anaesthesia or death by the most careful processes may render immune plants susceptible, and if such immunity is due to the action of vital antibodies the technique of tissue maceration, the death of the cells, the mixture of many substances which in nature are separate, and the irreversible modification of many others must necessarily lead to the

final obtaining of a sap or extract which differs very fundamentally from the fluids of the living cell. This fact has been recognized by the various investigators who have attacked this problem. Carbone has attempted, but unsuccessfully, to avoid it by employing for testing the circulating fluids of the plant (xylem and phloem currents). But thus far no one has been able to use *in vitro* a fluid from plants comparable for serological purposes with the animal blood. We are at an *impasse* in this direction. It may be that it will not be possible by zoöimmunitary techniques to add to our analysis the final serological proof. It may be, on the other hand, that a satisfactory technique can be devised. Perhaps methods of micro-manipulation or the use of large unicellular organisms such as *Valonia*, *Halocystis*, or *Caulerpa* may afford the answer. Meanwhile, however, it seems that, in view of the very strong evidence for acquired immunity in parasitism which has been derived from several sources, and in view of the profoundly atypical conditions surrounding the negative serological tests, the latter do not present an insurmountable barrier to the thesis under discussion. It would be highly enlightening and satisfying if the serological tests did conform to the experiments with living plants, but that they do not does not offer a significant refutation to the extensive evidence secured from studies in reinfection, morphology, host-specificity, and parasite localization as discussed in the earlier parts of this critique of acquired immunity in parasitism.

VIII. ACQUIRED IMMUNITY IN SYMBIOSIS

We have seen from the discussions of the foregoing sections that the theory of acquired immunity in plants is derived from observations and experiments in the injection of plants with foreign bodies and in the behavior of plants in parasitism. Symbiosis, which from one point of view is a controlled and non-injurious form of parasitism, affords a final source of evidence upon this theme, and indeed much of the earliest and strongest evidence has resulted from such studies as those of Bernard on the orchid symbiosis and of Cappelletti on the symbiosis in leguminose root tubercles. First, both in order of time and in immunological importance, will be discussed the results of the orchid studies, and this will be followed in turn by consideration of the symbiosis in the root tubercles of legumes, of other natural symbioses, and of the artificial symbiosis of the graft-union, all of which contribute to our knowledge of acquired immunity in plants.

A. Symbiosis in the orchid mycorrhiza

For fully fifty years the peculiar behavior of the mycelium of orchid mycorrhiza in the host tissues has been described and discussed. As early as 1886 Wahrlich (181) came to the conclusion that "the yellow clumps which are found in the root parenchyma of orchids are not plasma balls and do not belong to the host tissue but to the orchid fungus, and are true haustoria, later surrounded by hyphae." The significance and fate of these balls of hyphae within the host cells were not further understood at this time, however.

Wahrlich having noted the presence and distortion of the fungus mycelium within the orchid cells, it remained for Dangeard and Armand in 1897 (55) to call attention to the fact that the host cell is not passive during its invasion but that its nucleus becomes amoeboid, being active in passing from the ball of hyphae in the center of the cell to the periphery of the cell where it may assume various forms. Our first suggestion as to the immunological proc-

esses in the orchid mycorrhiza is due to Magnus who in 1900 (108) found that there are in the orchid two reactive types of cells, "host cells" in which the fungus never degenerates but which appear to serve as sources of nutrition for the mycorrhiza, and "digestive cells" in which the fungus first enters as normal haustoria which latter eventually become gnarled, clumped, skein-like, and finally die and are dissolved or digested. Meanwhile the host protoplast is not killed although it may become highly vacuolate, and the host nucleus may become hyperchromatic and amoeboid.

Bernard's memorable series of studies commenced with an analysis of the rôle of mycorrhiza in tuberization in 1902 (13). He determined that there are three types of tuberization: precocious and permanent tuberization with mycorrhizal infection at the beginning of seed germination and extending throughout the life of the plant as in *Neottia*, precocious and periodic tuberization with infection at the time of germination followed by alternate periods of tuberization (with mycorrhizal infection) and non-tuberization (without mycorrhizal infection) as in the *Ophrydeae*, and late and periodic tuberization such as occurs in the potato (wild) with infection and the resultant tuberization occurring only at maturity. Bernard concluded from these studies that tuberization is the result of mycorrhizal infection and that in its action the fungus may act at a considerable distance through the agency of soluble products. Further early descriptions of the behavior and function of mycorrhiza apart from those of direct immunological interpretation are to be found in such works as those of Gallaud in 1905 (65) and Burgeff in 1909 (28).

In 1904 appeared the first work of Bernard dealing directly with immunity in the orchid mycorrhiza (14). He found that among orchids *Bletia hyacinthina* is anomalous in that the embryo at first shows an almost complete immunity to the mycorrhizal symbiont, while later it not only becomes capable of infection but will grow no farther unless infected. The immunity takes the form of a precocious and very active digestion of the hyphae, which are able to enter the tissues unimpeded. By 1908 (15) Bernard had succeeded in obtaining non-virulent strains of the mycorrhizal fungi, which strains if inoculated into the orchids could invade the tissues but could not cause germination.

The following year in two very important papers (16, 17) Bernard reached the culmination of his studies on acquired immunity in the orchid mycorrhiza. His findings may be briefly summarized in the following terms. Mycorrhiza in the orchids has probably evolved from an active parasitism in the past. The fungi involved belong to genera characterized in many cases by virulent parasitism (*Nectria*, *Hypomyces*, *Rhizoctonia*). On the first entry of the fungus there is a rapid and unchecked invasion of the host tissues. This is soon opposed, however, by an acquired immunity which lasts for some time and inhibits secondary infection. If the first fungus inoculated is capable of forming a permanent association with the orchid, this resistance to reinfection is permanent, but if it is not adapted to such a consortium, the period of resistance to reinfection is only temporary and a second infection may occur. The immunity displayed by the orchid in checking and controlling further spread of the fungus within its tissues is of two sorts, a normal phagocytic immunity and an acquired humoral immunity. The phagocytic immunity is displayed particularly by certain specialized cells which lie in the deeper parenchyma

and in which the lobed nuclei are able to surround and digest the progressing mycelium. The humoral immunity, which is acquired as a result of the stimulation of the advancing mycelium, results first in a clumping or gnarling of the hyphae within the cells, which hyphae subsequently become dissolved or digested. The acquired immunological nature of this humoral immunity was demonstrated by experiments *in vivo* (18). Pieces of infected orchid tuber if placed upon sterile agar secreted substances which diffusing out through the agar not only checked the advance of a pure mycelium of the mycorrhizal fungus upon the agar, but even killed it back. Older tubers showed a more abundant production of the controlling substance than younger tubers. The toxic substance was thermolabile since it lost its toxic effect on heating to 55°C for 35 minutes. A certain degree of specificity was displayed by this diffusable substance since its action was directed in the main against the specific fungus infecting the tuber.

Bernard's work was confirmed in 1923 by Nobécourt (134), who repeated Bernard's experiments on the diffusability and nature of the humoral substance secreted by infected orchid tubers. He again observed the controlling and checking action of such a diffusable substance and further tested the question of whether the toxic substance pre-existed in the tuber before placing it on the agar. This was accomplished by subjecting the tubers to cold (−15°C) and chloroform vapor. Such a process decreased the reactivity of the tuber and the effect was believed by Nobécourt to be upon the cell and not upon the antibodies, which latter he therefore assumed were not pre-existent in the cell. But Magrou in 1924 (113; see also Magrou, 112 and 114) asks the question: Why were not antibodies pre-existent in the cells since the cells were previously infected by the mycorrhiza? His answer to this question was obtained by placing a piece of tuber for two weeks on an agar slant and then removing it and planting the slant with the specific fungus, *Rhizoctonia* sp. The result was that the fungus grew very poorly and then in a direction opposite to that in which the tuber fragment had lain. Magrou therefore concluded that the antimycorrhizal substance first demonstrated by Bernard and later confirmed by both Nobécourt and himself was pre-existent in the infected tuber, as would necessarily be the case in a true acquired immunity in the orchid mycorrhiza.

Bernard's findings on the morphology of the orchid mycorrhiza and his conclusions as to the acquired immunological nature of the orchid immunity have also been supported by the experiences of numerous others, among whom should be mentioned Ramsbottom (144), who confirmed the effects of vaccination of orchid tubers although he failed to observe phagocytosis, and Magrou (111–114, 116, 118).

We thus see that there is a complete body of evidence, repeatedly confirmed by various investigators, regarding the rôle of acquired immunity in the orchid symbiosis. It is plain from this evidence that the orchid tissues oppose the progress and potential parasitism of the fungus symbiont by means of two mechanisms, one a normal property of the host cell (phagocytosis), the other an acquired humoral mechanism in which, due to the stimulation of the fungus secretions, noxious and inhibitive and even lethal specific substances are produced by the host. These substances possess the properties of animal immune bodies, and their presence and nature have been determined by experiments both *in vivo* and *in vitro*. We may accordingly conclude that here in the orchid mycorrhiza we have a complete and

satisfactory proof that plants may show a defense mechanism homologous with that of animal serology.

B. Symbiosis in leguminose root tubercles

The study of immunity in the root tubercles of Leguminosae has likewise been extremely productive of evidence supporting the thesis that plants may show acquired immunity of the zoöimmunitary type. Here, as in the preceding case, such evidence is both morphological and serological.

It has long been known that the root tubercles of legumes contain symbiotic bacteria which on first infection are normal but which as the tubercles grow larger assume various atypical forms, passing through a pre-bacteroidal stage of swelling to a bacteroid stage in which they assume X and Y and arbuscular forms and are greatly enlarged. The immunological significance of this was first pointed out by Hiltner and Störmer in 1903 (73, 74). These investigators came to the conclusion that the reactions of host and bacteria are best explained in the terms of a partial or controlled active immunity, this conclusion being based upon the facts that in the expressed sap of leguminose plants there is a substance which when added to bacterial colonies causes plasmolysis and disintegration of the bacteria, and that inoculation with a virulent strain of bacteria prevents the possibility of later infection with less virulent bacteria.

The theory of Hiltner and Störmer was confirmed in principle, although criticised in certain details of the interpretation, by Süchting the following year (169). Süchting likewise recognized the acquired immunological character of the relationship here as may be seen from his remark that "there is here in plants a production of prophylactic substances, antibodies, just as the bacteria form toxins or infectious substances." He further supported the theory of acquired immunity in this symbiosis by his observation that there is a definite limit to the number of tubercles which may be formed, regardless of the amount of inoculum introduced, this limit being conditioned by an immunological equilibrium within the plant. This is a situation strikingly reminiscent of that found by Kunkel in cabbage club-root as described above.

For the most complete and extensive work on immunity in the leguminose root tubercles we are indebted to the studies of Cappelletti in the years 1923–1928 (29–34). Cappelletti made a careful investigation of the morphology of the tubercle bacilli in comparison with the serological behavior of the host extracts. He found that in their reactions toward the bacteria the Leguminosae comprise two distinct types. In one type, typified by *Pisum*, bacteroids are formed accompanied by nuclear disturbances and the production of antibodies in the tubercles specifically directed against the bacteria. In the other type, typified by *Phaseolus*, bacteroids are not found, and neither are antibodies demonstrable in the tubercle saps. The antibodies found manifest the usual thermolability of animal antibodies, being destroyed by heating for one-half hour at 78–80°C. There is a clear correlation between morphology of the bacteria and serological reactivity of the host. Bacteroids are present in the tubercles only at maturity of the plants, from the period of inflorescence on. Agglutinins and precipitins are likewise present only at this time, being absent in the younger tubercles which contain no bacteroids. If inflorescence is prevented one observes a new development of tubercles in which agglutinins are evident although not abundant. If the plant is then left alone new flowers are formed, complete bacteriolysis occurs,

and there is a rapid and notable augmentation of the agglutinins. The antibodies formed appear to be strictly localized in the infected cells. Thus if the tubercle bacteria occur in the intercellular cavities in the tubercles they fail to assume the bacteroidal form (Dangeard, cited without reference in 32).

Cappelletti's work shows that there is a complete and harmonious correlation between the abnormal morphology of the bacteria and the presence of antibodies of the zoöimmunitary type. Here as in the case of the orchid mycorrhiza the work is relatively complete although there are still a few perplexing questions to answer. Among these may be mentioned the lack of conformity between Cappelletti's theory of localization of the antibodies and Süchting's finding regarding the inhibition of new infections by pre-existing tubercles. Moreover Kořínek (81) was unable to demonstrate agglutinins in root tubercles of Leguminosae, perhaps because he was dealing with Cappelletti's *Phaseolus* type, or because he was testing at a period before the appearance of the antibodies, i.e. before flowering. Němec, on the other hand, has observed agglutination or a phenomenon resembling it *in vivo* in leguminose root tubercles (132). Another problem is raised by the discovery of Zipfel (191), Barthel (8), and others that the bacteroidal form may be induced in artificial culture by the addition to the culture media of such substances as caffein, glucosides, certain carbohydrates, inorganic substances such as saltpeter and phosphates, and organic acids and their salts. This does not necessarily contradict Cappelletti's theory, since it is well known that the various types of serological reactions in animals may be simulated or reproduced by non-immunological causes, but it requires that one exert his utmost caution in deciding whether a given reaction is or is not immunological.

However, the burden of Cappelletti's argument appears clear and complete. His observations *in vivo* are thoroughly supported by his serological tests, and the latter give evidence that he was dealing with reactions of the zoöimmunitary type. Accordingly, we may with safety add the case of the leguminose root tubercles to that of the orchid mycorrhiza as a second sound body of evidence supporting the thesis of acquired immunity in symbiosis.

C. Other natural symbioses

No other natural symbioses have been studied from the immunological viewpoint with a fraction of the thoroughness with which the orchid mycorrhiza and the Leguminosae have been. Yet numerous other types of symbiosis do occur in nature and these have in many cases been studied morphologically at least. It is accordingly instructive at this point briefly to report such findings in these other natural symbioses as relate to the investigations discussed above.

The mycorrhizae of Solanaceae have been somewhat more thoroughly investigated in this connection than symbioses in other groups and served as the material which led Bernard to his theory of the dependence of tuberization upon symbiosis (13, 19). In solanaceous tubers Magrou (109, 110, 113, 115) found present the same type of phenomena as have been found to be of immunological significance in the orchid mycorrhiza, such as the clumps of mycelium within the host cells which were later digested by the host protoplast. Phagocytosis was also observed within the cells, but this normal mechanism of immunity, according to Magrou, seemed insufficient to control satisfactorily the invader, and the localization of the mycorrhiza in the host tissues appeared to be the result of an acquired humoral immunity comparable to that in orchids. Magrou's experiments have been criticized

by Ducomet (in Magrou, 113), who claimed that Magrou had used too few plants, plants of variable stocks and unsuitable age, and incorrect interpretation of numerical data. Magrou's answer to this criticism of Ducomet, however (113), appears to justify Magrou's work.

The clumping of mycorrhiza mycelium followed by its death and digestion by the host as observed in orchids and Solanaceae has been likewise seen in a variety of other symbioses. Janse in 1897 (76) described such hyphal abnormalities in a wide variety of mycorrhizae including hepatics, Lycopodiales, Selaginellales, ferns, gymnosperms, monocotyledons, and dicotyledons. Shibata in 1902 (157) extended the same findings to include *Podocarpus*, *Psilotum*, and *Myrica*. Similarly clumping of the mycelium, phagocytosis, and digestion have been observed in hepatics by Gallaud (65) and Magrou (117), in *Arum* and *Paris* by Gallaud (65), in *Calluna* by Rayner (148), and in *Lathyrus* and *Mercurialis* by Magrou (111). Magrou's studies on *Pellia epiphylla*, an hepatic, are of particular interest, since here the observations are in considerable detail and appear to show that the localization of the mycorrhiza within the host thallus is controlled by fungicidal substances secreted by the reproductive portions of the plant. Active phagocytosis occurs but in addition to this there seems to be an active humoral immunity which checks the growth of the mycelium as it grows toward the sporogones and archegones.

Finally in lichens analogous phenomena have been recorded by Moreau (123, 124). In *Ricasolia* it frequently happens that algae (Cyanophyceae) not belonging normally to the lichen thallus come in contact with the lichen thallus, which forms about them tubercles known as cephalodia. These may be either internal or external and represent a temporary, unstable symbiosis or parasitism in contrast to the normal, permanent lichen symbiosis. Within the cephalodia the foreign Cyanophyceae are gradually killed and dissolved, a process compared by Moreau to the killing and lysis of foreign bacteria in the animal body, and attributed to a defense reaction presumably of the type in which we are here interested.

We thus find that the orchid and lichen symbioses are by no means isolated cases of acquired immunity in symbiosis. Comparable or identical phenomena occur throughout a very wide range of plants, including all of the four major plant subkingdoms. It would thus appear that acquired immunity of the type demonstrated in the higher plants is a very widespread phenomenon, an attribute of living matter at all levels of plant as of animal life. Such a conception is based to some extent upon analogy, but it would seem that the analogy is justified in view of the large number and wide range of perfectly confirmatory observations. That acquired immunity of the zoöimmunitary type plays a fundamental part in the control of the potentially parasitic symbiont is manifest in both cases which have been studied in detail, and in conjunction with all the other types of evidence preceding offers a final proof that the ability for an organism to respond to the stimulus of foreign bodies by acquired humoral reactivity is an attribute not of the higher animals alone but of life in both kingdoms.

D. The graft-symbiosis

The graft union is an artificial form of symbiosis, since stock and scion are mutually interdependent. In the graft union two tissues of different origin are brought into intimate mechanical and physiological contact. It might therefore be expected that the graft union would offer an excellent opportunity for studying acquired immunity, since each graft-symbiont would be expected to sensitize the other in an

antigenic manner leading to the elicitation of antibodies in each symbiont against the other. This conception was made the basis for an extensive series of investigations by Kostoff in 1928–1931 (82, 84, 86, 87, 88, 90). This type of work has been subsequently investigated by Silberschmidt in 1931 (161) and by Whitaker and Chester in 1932 (187).

Kostoff's experiments were performed with numerous genera and species of Solanaceae, which family is well adapted to graft and cytological techniques, and they included morphological, cytological, and serological findings which appeared to be mutually confirmatory in demonstrating the presence of antibody-formation in such grafts. Kostoff's morphological evidence of acquired immunity in his grafts included his observations that repeated grafting upon the same stock is not possible since although a first scion may successfully graft upon a given stock, a second grafting of a similar scion upon the same stock may be attained with difficulty or wholly inhibited, that the grafted plants frequently showed morphological malformations such as galls, and that grafted scions often showed abnormal corollas and calices. His cytological evidence comprised the finding of irregular and abnormal meioses, the failure of starch to cross the graft union, and agglutination of the plastids of cells near the graft union (83, 84, 87). This morphological and cytological evidence was supported by two types of serological investigation, namely investigation of the mutual precipitin potency of extracts of stock and scion (as determined both by gross reading of ring tests, and by the more delicate nephelometric method of measurement) and of the mutual lytic activity of stock and scion (as determined both by gross observation of lytic rings and by the dialysis-Ninhydrin technique which is based upon a chemical, colorimetric determination of the amount of protein-cleavage-products before and after lysis). These various types of serological investigation were found by Kostoff to agree in demonstrating that in a few of his graft unions there was an increase in precipitin and lytic potency of stock toward scion and of scion toward stock after grafting, an increase which was strongest near the graft union, weaker farther from it, which increased to a maximum at about one month after grafting, and which exhibited a partial but imperfect specificity. Kostoff believed that his serological results served to explain the morphological and cytological results, and that taken together these offered a complete demonstration of acquired immunity in grafted plants.

Silberschmidt in an excellent discussion has reviewed Kostoff's work and offered numerous suggestions based upon the assumption that Kostoff's reactions were truly immunological protein reactions. Silberschmidt, however, in his few exploratory grafts failed to obtain any significant rise in precipitin potency due to grafting.

In a second contribution (161a) Silberschmidt has reported further investigations of the Kostoff reactions. Although some positive results were obtained, the "acquired precipitins" found were not specific, and because his investigations gave no foundation for the assumption of the existence of specific toxic substances in the grafted scions, Silberschmidt challenges the theory of the gradual immunization of the scion by the stock, at least for the graft combinations investigated by him.

Meanwhile Chester and Whitaker (51, 52, 53) had been engaged in a study of the nature of the reactions believed by Kostoff and Silberschmidt to be serological. Their study showed the "precipitin" reac-

tions in the Solanaceae to be non-immunological in character, due to non-protein substances normally present in the cell, while such observation as they made of the "lytic" reactions (ring tests) revealed the occurrence of such lytic rings in non-immunological extract layerings. Continuing their work these same investigators next studied the behavior, morphological and serological, of grafted Solanaceae (187) and found that in none of the cases tested was there any significant alteration of the "precipitin reaction" after grafting, nor was there observed any production of the morphological and cytological abnormalities reported by Kostoff. The work of Whitaker and Chester was more extensive than that of Kostoff as regards the number of species grafted, the number of grafts tested, and the variation of conditions attending extraction and testing.

It therefore appears that this technique of investigation which looked so promising is not adapted in its present form to the study of acquired immunity in plants. The "precipitin" tests which have been found in normal plants are non-immunological, the acquirement of true precipitins after grafting has not been demonstrated, and the gross observations of the "lytic" reactions have shown them to be either non-immunological or at least simulated by non-immunological reactions. There remain of Kostoff's serological investigations his dialysis-Ninhydrin results which have as yet not been repeated by other workers and which for this reason and in view of the "pseudo" nature of all his other reactions are to be accepted for the present only with reservation. Moreover his findings with regard to the morphology and cytology of the grafts have not been substantiated by others. The effects described by Kostoff, gall-formation, abnormal meioses, corolla and calyx deformity, etc., are highly suggestive of environmentally conditioned characters rather than specific antigen-antibody effects. The inability to regraft after a preliminary grafting may well have been due to the greater maturity of the tissues at the time of the second operation, since Whitaker and Chester report that grafting of the Solanaceae is much more easily accomplished with succulent young tissues. The agglutination of plastids *in vivo* may have been immunological; it may equally well have been due to a variety of other causes, such as cytological methods or nutritional disturbances about the graft union. In a word, there appears to be little or no sound evidence to support the contention that acquired immunity has thus far been demonstrated in grafting.

The failures in demonstrating this point, however, are not detrimental to the conception that acquired immunity does occur in plants. They are instructive in showing us the limitations of our present techniques and the dangers of jumping to hasty conclusions on the basis of imperfectly understood observations. Just as the expressed-sap method has failed to reveal antibodies in parasitism, so for the same reason does it appear to be unsuited to a study of acquired immunity in the graft union. It may be that refinements of the technique will reveal the possibility of demonstrating antibodies in grafted plants, or it may be that sensitization in such cases is far less effective than in parasitism and in other forms of symbiosis, so that there is little or no production of antibodies in such cases. This last would not seem unlikely when one considers the success of many interspecific grafts.

Closely allied to the subject of acquired immunity in grafting, although not dealing precisely with symbiosis, is the subject of hybridization. In hybridization there is the bringing together of two foreign protein systems, and it might be that

here acquired immunity could play a part in the success and subsequent behavior or failure of hybrids. This is a problem to which Kostoff again has contributed (84, 85, 89). He found that certain species hybrids were characterized by tumor formation, and that this tumor formation was correlated with a "precipitin" difference between the parents. Unfortunately, however, the results with the "precipitin" tests are subject to the same criticism as that applying to his grafting experiments, and since there thus remains no proof as to the serological difference between the parents the correlation with tumor formation is not significant. Likewise, and for the same reason, Kostoff's contention that serological differences may serve to explain the appearance of cancer in humans is as yet without basis from the standpoint of plant serology. Again we may say that this offers no proof that immunological phenomena may not play a part in the success and behavior of plant hybrids; we may merely conclude that such has not yet been demonstrated.

In concluding the present section we may briefly recapitulate the findings of our analysis of acquired immunity in symbiosis. We have seen that there is clear-cut and abundant evidence that the orchid controls the distribution and activity of its mycorrhizal symbiont by the production of antibodies of the serological type. There is likewise good evidence that the same applies to the action of Leguminosae toward their symbiotic tubercle bacilli. A survey of the occurrence and nature of symbiosis in many of the other plant groups including Thallophyta, Bryophyta, Pteridophyta, and Spermatophyta shows that although the complete proof has not been offered in other cases than those of the orchid and legume symbioses, yet in all these other types of symbiosis phenomena closely analogous to those of the orchid and legume symbioses occur, and it therefore seems probable that acquired immunity as observed to control the orchid and legume symbioses also occurs generally in symbioses throughout the plant realm. On the other hand, the investigations of acquired immunity in graft unions and hybrids of the Solanaceae have proved that these are not adapted to the demonstration of antibodies according to our present techniques, although this is by no means detrimental to the significance of the other findings in this paper regarding the occurrence of acquired immunity in plants.

IX. THE SIGNIFICANCE OF ACQUIRED IMMUNITY IN PLANTS

Having completed an analysis of the experimental findings in the field of acquired physiological immunity in plants we are now able to turn this knowledge to account by a study of the theoretical and practical significance of these findings. The present section will therefore treat of the significance of acquired immunity in plants with emphasis in turn upon the proof of the existence of acquired immunity in plants, the nature of this immunity, its rôle in phytopathology with particular regard to the part played by acquired immunity in the evolution of parasitism, in epidemics and natural control, and in host-parasite relationships, the practical applications of acquired immunity in phytopathology, and the direction of future research in this field.

A. The existence and nature of acquired physiological immunity in plants

The main question which has concerned investigators in this field has been: Does acquired immunity of the animal type occur in plants? The present analysis has yielded a definitely affirmative answer to this question. There are a host of experi-

ments and observations regarding parasitism and symbiosis which have led clearly to the conviction that plants may protect themselves from foreign invaders by the elaboration of specific substances directed against the intruder. The bases for this conception are the facts as demonstrated above that plants recovering from a first attack of a parasite show a resistance to a second infection by the same organism, that experiments in both active and passive vaccination have revealed in practically all cases the protection afforded by such treatment, that the behavior of the parasite within host tissues, the host-specialization of plant parasites, and the localization of parasites within their host are all better interpreted as antigen-antibody effects than in any other manner, and that the experiments on various types of symbiosis have proven that the types of symbiosis studied in detail are indubitably made possible by an acquired immunity of one symbiont toward the other, while the evidence regarding other symbioses in plants shows that this condition of acquired immunity in symbiosis is of very general occurrence throughout the whole of the plant realm.

With the exception of the studies on symbiosis the evidence for the acquirement of physiological immunity in plants has been almost entirely drawn from experiments and observations with living plants. Serological tests *in vitro* have with this exception yielded either negative or conflicting results. To the zoöimmunologist this might appear an insurmountable objection to our thesis. But the foregoing analysis has shown that we cannot unreservedly transfer all of the principles and techniques of animal serology to the field of plant immunity. We must devise new methods of attack and must be awake to the possibility of distinct manifestations of acquired immunity in the plant realm. It appears that there is one important barrier, not to the principle of acquired immunity in plants but to the application of animal methods to plants, namely the lack in plants of a circulating stream analogous to the blood stream. In both kingdoms the living cell is undoubtedly the reactive unit responsible for the production of antibodies. In animals in addition there is the blood stream, which serves at once as a medium for accumulation, transportation and demonstration of the antibodies. In plants there is no question of the production of the same type of immune bodies as in animals, but plants have no comparable medium for accumulation, transportation, and demonstration of such bodies. The result of such a situation would necessarily be that the antibodies in plants would be more strictly localized within the infected tissues and that demonstration of them would necessarily involve the use of the living cell. Thus far all of the experiments in the demonstration of plant antibodies which have given inconclusive or negative results have employed the techniques of either expressing the sap of plant parts or of macerating plant tissues in such solvents as water and physiological saline solution. In either case the cells are killed, substances discrete in nature have combined, and many substances have experienced irreversible change. This has been considered to be an application of animal serology to plants but it is far from that. Experiments on anaesthesia of plant cells and on the most gentle methods of killing plant cells have revealed that the immunity of the cells is lost not only on the death of the cells but even on their temporary narcosis. There is therefore no more reason for regarding the negative results of the "serological" tests in plants as evidence disproving the thesis of plant acquired immunity than there would be for expecting to obtain evidence as to the

cytology of the apple fruit from a microscopic examination of cider.

Acquired immunity in plants is a vital phenomenon. It is a function of the living cell and it must be studied in the living cell since plants have no such mechanism as animals for serological study. This is not an impossible requisite. Bernard has shown how the serology of the living orchid cell may be studied. Micrurgy is another point of attack. The artificial culture of living tissues in vitro may likewise afford an aid in this direction, and doubtless other techniques will be devised. Suffice it to say that there is abundant evidence thus far from the study of living plants and tissues that the acquirement of immunity to foreign bodies is a function not of animals alone but of life. In plants it is manifested chiefly or entirely in the reactions of living cells, which leads to a somewhat stricter localization of immunity than in animals. This implies that in plants one must attack the problem from the standpoint of the living cell. The techniques and the principles of the rôle of acquired immunity in plant life must both start from this basis.

It is not meant to be implied that there is no circulation of the antibodies in plants. Undoubtedly there is some such circulation, although it must be very limited as compared with that in animals. It may be that such circulation operates directly through the protoplasmic cell connections, and it is also not impossible that the circulating saps of the plant may serve to a limited extent as media for the transportation of antibodies. This latter possibility has been particularly investigated by Carbone and Arnaudi (45–47) but thus far without conclusive results. Be that as it may, there is assuredly no close analogy between such antibody circulation and that in animals and we are accordingly compelled to direct our attention in the main to the behavior of living immunized cells.

B. The rôle of acquired physiological immunity in phytopathology

We have seen that acquired physiological immunity is exhibited in an important and widespread manner in parasitism and in that special branch of parasitism, symbiosis. In nature there is no question, from the findings reported above, that such immunity is a common and ubiquitous physiological property of plants. This being so it must exert an important influence upon the occurrence and severity of plant disease in nature. In what respects and to what extent does it influence phytopathology? Light is shed upon this question by the following considerations.

Most plants are immune to most parasites. In a great many cases this general immunity is due to normal properties of the plant, such as the impervious character of the superficial tissues or the unfavorable external or internal environment of the plant. In many cases, however, we have submitted evidence to show that the defense of plants against parasites which in nature do not succeed in the parasitism of such plants is due to an acquired defensive reaction set up in the host as a reaction to the stimulus of the invader. That such a mechanism is responsible for a considerable amount of the relative immunity in nature is seen from the frequency with which one is able to demonstrate in host tissues the checking and killing of the vegetative body of the parasite. To be sure acquired immunity is only one of the protective mechanisms of plants. It is a mechanism which reaches its highest development in suscepts related to the natural host, where normal defenses are less abundant, and where immunity is distinctly relative. But in the evolution of parasitism tentative attempts at increasing this host range must be continually being made by parasites, and these attempts would naturally be chiefly directed

toward suscepts closely related to the natural host. It is in just such cases that acquired physiological immunity is most evident, and it naturally follows that acquired immunity must play a significant part in the host restrictions of parasites.

Passing to a broader aspect of acquired immunity in parasitism it is of interest to study the relation of acquired immunity to the epidemic occurrence of diseases. A regular cycle of progress marks the bringing together of new host-parasite combinations. If the conditions are favorable for parasitism and spread of a given pathogen, the disease very rapidly increases after its introduction. There eventually occurs a period of the height of epidemic severity which may or may not prove fatal to the host taken as a whole. If the host is not eliminated, eventually this epidemic severity begins to decrease until it reaches a steady point with little or no variation beyond that due to environmental and local factors. We must distinguish here between epidemics due to facultative parasites and those due to obligate parasites. In the latter case some degree of immunity is indispensible to the perpetuation of the disease since only living hosts may serve as substrata for the parasite. We must also distinguish between the diseases of annual and those of perennial plants. In the perennial plants the duration of life is so great as to permit several or many successive attacks of the parasite, and accordingly the opportunity for acquired immunity to function is considerably greater than that in annuals. We see then that acquired immunity would be expected to exert its greatest action in the case of diseases of perennial plants, notably trees, and in diseases caused by obligate parasites, e.g. the powdery mildews, the rusts, and the Exoascales. Indeed the observations which have been made of acquired immunity in nature have centered about these types of disease.

The effect of acquired immunity in checking the severity of epidemic tree diseases has already been mentioned with respect to the *Oidium* disease of oak, the *Gymnosporangium* rust of red cedar, the *Endothia* canker of chestnut and the *Hemileia* rust of coffee. It is thus apparent that in such diseases in nature the successive infections of trees result in some degree of acquired immunity which is expressed by gradual tolerance of the parasite, alternation of periods of infection and freedom from infection, increased age of coppice growth of infected trees before succumbing, and decrease of severity of attacks in the four cases mentioned. We see, accordingly, that although acquired immunity may or may not play a major rôle in the normal freedom of plants from disease, it does play a leading part in the gradual checking of epidemics of plant disease, a rôle which combined with natural selection of resistant plants serves to save the parasitized species from extinction.

From the results of this analysis it is also evident that acquired immunity has had a part to play in the evolution of parasitism and symbiosis. The nature of the relationship of the orchid to its mycorrhizal symbiont and of the host to its obligate parasite are exceedingly delicate and are conditioned by a precise acquired immunity of such a nature as to permit the survival of both members of the association. Evolution of the symbiotic and parasitic habits respectively has been governed by evolution of this property of delicately adjusted partial immunity. We do not need to look far to find many cases of thwarted parasitism and symbiosis, the lack of the adjustment being due to a lack of the proper immune relationship between higher plant and fungus. In the rusts such thwarted attempts are seen in hypersensitivity, where the immunity is too weak, and in the small abortive lesions which have been shown above to

be due to a precocious and too great acquired immunity. Likewise in the orchid symbiosis cases have been recorded where the union is unsuccessful because of the immunity deficiency on the part of the host or excess virulence on the part of the fungus, leading to virulent parasitism, or the converse in which case germination fails to occur. Evolution of the parasitic and symbiotic habits in these two types of association, which assuredly represent the end results of long periods of adaptation, must thus necessarily have been concerned with the evolution of virulence on the part of the fungus and of the ability to control this virulence through the mechanism of acquired immunity on the part of the vascular plant.

C. *Practical applications of acquired immunity in phytopathology*

In human medicine an application of the principles of acquired immunity has afforded some of the greatest practical aids in curing and preventing disease at the disposal of the physician. No such great practical advantage can be prophesied for an application of acquired immunity in plants, however, because of the inherent difference in the purposes of plant and human pathology. The aim of human medicine is to preserve the individual; the phytopathologist, on the other hand, as a rule has little interest in the individual, his main objective being the preservation of the population. Moreover while much of the activity of the physician is devoted to cure or therapy, that of the phytopathologist is more directly concerned with prevention or prophylaxis. Yet in spite of this it is not inconceivable that the principles of acquired immunity in plants may have practical applications in pathology and that the science may have not only theoretical but commercial importance. In the forest, the plantation, and the crop field it is doubtful that much in the way of biological therapy and prophylaxis can be accomplished. In ornamental plantings, in seed beds, and in the greenhouse, however, where the value of the individual plants is much greater, a serious consideration of the application of the findings of acquired immunity is warranted.

Little or nothing has been done in a practical way in turning to account the results of investigations in this field. Some have even objected to such an application on theoretical grounds, basing their argument upon the frequently temporary character of the immunity. Yet numerous vaccination experiments have proven that plants may be immunized and in some cases strongly so by such treatment. Leemann (102) has pointed out that the resistance and susceptibility of plants may be varied by the treatment of the soil with various biological products. In such diseases as damping-off of seedlings, potato tuber diseases, and even possibly in diseases of shrubs and trees where the individual plant is worthy of treatment, there is a field for experiment in the practical application of the principles of acquired immunity. Sieden and Trieschmann (158) have made a start in this direction and have been able to increase appreciably the potato yield as a result of a relatively simple tuber treatment.

One cannot go far in theorizing on the practical outcome of the knowledge thus far available, particularly in view of the almost total lack of experiments in practical application. Even were such practical applications not found to be worth while, the theoretical contribution of acquired immunity toward interpreting and understanding various pathological and medical problems justifies the study of the field, but assuredly we have here a line of attack for empirical pathological

problems which must needs be carefully sounded out.

D. *The direction of future activity in this field*

During the course of this paper numerous suggestions have been made as to desirable lines of future investigation in the field of acquired plant immunity. They are concerned with several main problems, namely:

1. Further confirmation of the *occurrence* of acquired immunity by filling in the several gaps which exist in the body of experimental data, by extending the results of the earlier investigations to a broader scope, and by strengthening by more carefully controlled experiments the less conclusive stages in the argument. Reference to the several sections of this paper will afford specific illustrations of this, and no attempt will be made to enumerate them all below because the weaknesses of each section will be best made apparent to the reader by his own perusal of the assembled data. Specific directions with regard to the procedure in certain types of experimentation have been given.
2. A study of the *nature* of acquired immunity in plants. Very little has been done in a critical way in this phase of the work. The evidence indicates that acquired immunity in plants is a vital, cellular phenomenon. Such methods as tissue culture and micrurgy are indicated from this fact. Large-celled plants such as certain of the algae, the coenocytic fungi, and the Charales should prove valuable material in this connection. Because of the essential similarity of acquired immunity in plants and animals and because of the relative ease of investigation of plants as compared with animals in certain respects, this type of investigation should be of interest to the animal serologist.
3. The study of the *theoretical bearing* of acquired immunity in pathology. The inclusion of the concepts of acquired immunity within the theoretical considerations of the plant pathologist is certainly indicated by the findings thus far. The pathologist cannot neglect in his analyses the importance of this phenomenon as has been seen from our brief survey of the significance of acquired immunity in plants as set forth in the preceding section.
4. An investigation of the *practical applications* of biological therapy and prophylaxis. There is practically a total lack of such investigations and the preceding subsection has pointed out concrete problems confronting the pathologist which should be attacked from this standpoint.

X. RECAPITULATION

The present paper is a critical analysis of the problem of acquired physiological immunity in plants. It has been prepared in an endeavor to organize and clarify our knowledge in this important and difficult field of phytopathology by a determination of the occurrence and rôle in plants of defensive reactions of the zoöimmunitary type and of the theoretical and practical significance of such reactions.

In order to prepare the way for a clear understanding of the thesis, attention is given in an early part of the paper to the subject of immunological conceptions and terminology and to a short chronological account of the main steps in the develop-

ment of the concept of acquired immunity in plants.

On the basis of our knowledge of the factors conditioning acquired immunity in animals and of the physiology of plants, an analysis is made of the possibility of the occurrence of acquired immunity in plants as indicated by *a priori* deduction. The main *a priori* objections to such a thesis, i.e. differences between plants and animals with respect to circulatory system, manner of growth, opportunity for sensitization, and reaction toward disease, are in no case found to be valid objections, and on the other hand there are a certain number of facts which definitely lead to an *a priori* expectation of demonstrating acquired immunity in plants

In order to recognize and evaluate acquirement of antibody potency in plants it has been first necessary to investigate the presence and nature of normal plant antibodies. Such an investigation has revealed that antibodies of the zoöimmunitary type normally exist in many plants but that an identification of them is complicated by the frequent presence in plants of substances which exert actions simulating those of the true antibodies (pseudoantibodies). Thus both true agglutinins and pseudoagglutinins, true lysins and pseudolysins, and true precipitins as well as pseudoprecipitins have all been identified as normally occurring in plants. In addition to these there are present in certain plants growth-inhibiting substances which are probably of the pseudo type.

Acquired immunity in plants may be investigated by the artificial introduction into plants of foreign bodies, by a study of the reactions in parasitism, and by a study of behavior in symbiosis. The three subjects have accordingly been treated in turn with the following results:

Experiments in the introduction into plants of non-protein toxins have revealed that although the evidence regarding antitoxic effects in plants is very limited it seems probable that under some conditions at least plants can either acquire a tolerance to or actively combat foreign non-antigenic toxic material by reactions of the type of antitoxic reactions in animals. The artificial introduction of soluble proteins into plants has not been found by most investigators to lead to anaphylactic shock, although a very interesting phenomenon resembling this has been observed in sensitized bacteria. Beyond one observation of pseudoprecipitins no experiments have been performed to determine the acquirement of precipitins due to the injection of soluble proteins, an important phase of work which should be investigated. The evidence for the production of antibodies as a response to the introduction of particulate antigens is not wholly satisfactory because of the lack of completeness of most of the experiments, because of the action of unknown variables, and because of the presence of pseudoantibodies. The evidence is insufficient either to prove or to disprove the thesis under consideration but it is valuable in showing the dependence of acquired immune reactions upon the living state of the cell, in recognizing and allowing for the action of pseudoantibodies, and in directing future investigation in this field.

That immunity analogous at least to that of animal immunology may be acquired as a result of parasitism has been demonstrated by several types of investigation. In the first place the observations of many investigators are mutually confirmatory in finding that plants recovering from a first attack of a disease display a greater or less resistance to a second infection. This acquired immunity may in some cases be weak, temporary, or localized, and because of this and other difficulties in this type of investigation the need and requisites

for satisfactory demonstrations in this field are discussed in detail. Secondly, practically all of the numerous experiments thus far reported are in agreement in finding that the vaccination of plants, whether with attenuated strains of parasite, with extracts of parasite, or with antibodies of plant or animal origin, results in an increased and often very highly increased resistance of variable duration toward subsequent parasitic infection. Thirdly, the behavior of parasite and host when in contact has been found in many cases to be interpretable only in terms of an acquired immunity of the host toward the parasite. The same is true when one considers the complexity of the host specialization of certain parasites, notably the rusts, and the dependence of immunity upon a living, active condition of the host. Finally, the activity of plant hosts in restricting and killing their invading parasites is more satisfactorily interpreted by an hypothesis of acquired immunity of host toward parasite than by any other hypothesis yet advanced. In passing, the subject of hypersensitivity as displayed by the rust fungi is discussed in the light of its bearing upon the problem in hand. Serological demonstration of antibodies in parasitism has been almost universally unsuccessful, doubtless due to the difficulty of adapting serological techniques to plant materials and to the essentially vital nature of the substances responsible for the acquired defensive reactions observed in parasitism under the various conditions enumerated above.

Acquirement of immunity of the zoöimmunitary type in symbiosis has been thoroughly demonstrated in the behavior of orchids toward their mycorrhizal symbiont and of Leguminosae toward their root tubercle-bacilli, the demonstrations depending on both morphological and serological behavior. In addition analogous phenomena have been recognized in so many other types of symbiosis that the evidence strongly indicates a general occurrence of acquired immunity in symbioses throughout the whole of the plant kingdom. On the other hand, the graft-symbiosis has failed to prove satisfactory material for the study of acquired immunity in spite of the promise of early experiments.

On the basis of the experimental findings an analysis is made of the nature of acquired physiological immunity in plants. It has been shown that there is abundant evidence from the study of living plants and tissues that the acquirement of immunity to foreign bodies is a function not of animals alone but of life in both kingdoms. In plants it is manifested chiefly or entirely in the reactions of living cells, which leads to a somewhat stricter localization of immunity than in animals. This implies that the techniques and principles of the rôle of acquired immunity in plant life must start from this basis. Acquired immunity in plants has been found to play an important part in both plant disease and in symbiosis under natural conditions. It has important effects in limiting the host distribution of parasitic fungi, in checking the severity of plant disease epidemics, and in the evolution of highly specialized obligate parasitism and symbiosis.

The possibility of the practical application of the principles of acquired immunity in plants is discussed. It is found to be a desirable line of investigation, although little or nothing has yet been done in this field, and accordingly suggestions are made as to the practical advantage which may be taken of acquired immunity in plants.

Finally a number of suggestions have been made as to the direction of future activity in this field of study. The desirability of investigations regarding the occurrence, nature, theoretical bearing, and practical applications of acquired plant immunity are outlined and discussed.

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ADDENDUM

(Literature bearing on the theme of this review but received too late to be incorporated into the text.)

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MY UNCLES, LOUIS BEDEL AND HENRI D'ORBIGNY

By MAURICE BEDEL

NOTE

This sketch of two distinguished French entomologists appeared in the centenary volume of the *Société Entomologique de France* (1932, pp. 95–99). The author, Maurice Bedel, has courteously given me permission to translate this tribute to his uncles. He is himself an entomologist, though better known as the author of three charming and humorous novels, "Philippine," "Monsieur Molinoff" and "Sulphu." W. M. Wheeler.

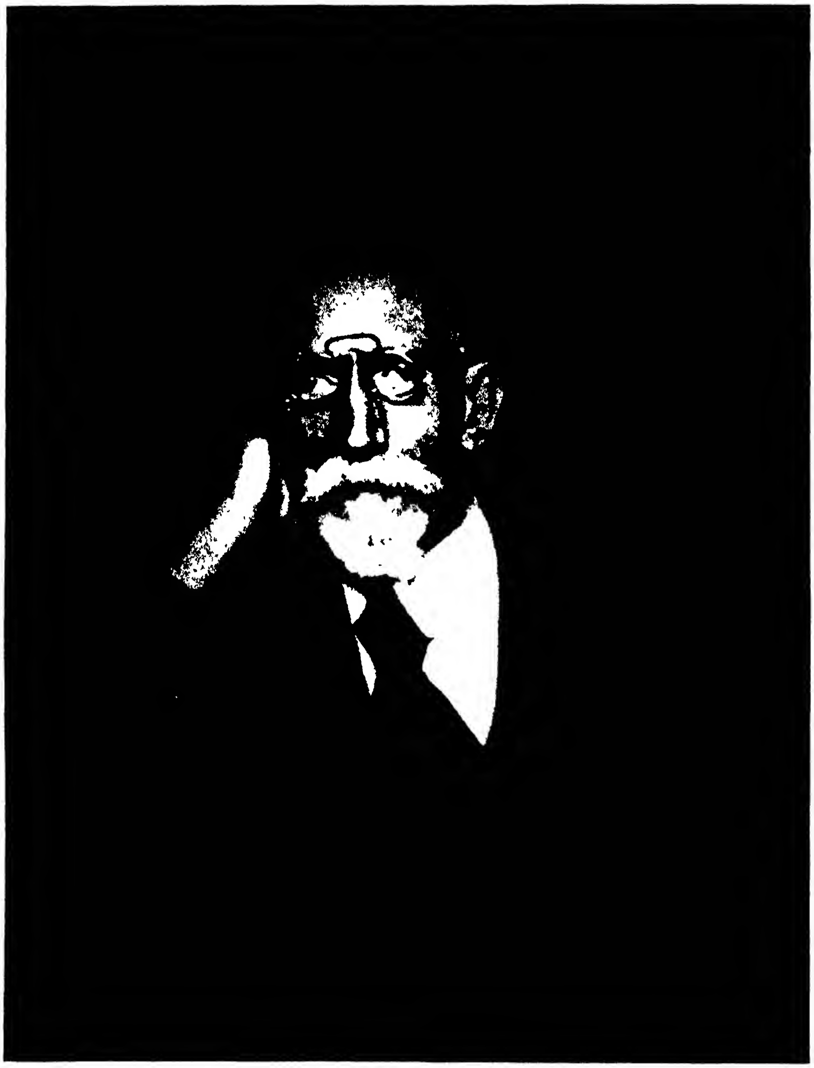
MY GRANDFATHER was a councillor of the court and a lepidopterist. As soon as he could doff his red robe, he seized his green butterfly net and ran about in the forest of Meudon, where, seventy-five years ago it was still possible to pursue butterflies without risk of falling into an ambuscade of boy scouts. My father and my uncle Louis accompanied him. My father, being an artist, delighted in contemplating the tiger-beetles along the sun-lit paths, while my uncle pursued the ravishing beasties and popped them into his bottle, because his youthful brain was already seething with the catalogues and synopses which were later to make him famous. Thus arose, between the two brothers, the differences which were only to increase during the course of their lives, till they lost each other from view forever.

My uncle remained a mystery to me till my father's death, when I was sixteen. He was described to me as a man devoid of sociability, preferring the tables of the cafés of the Boulevard Saint Michel to the family board, frequenting during the summer the inns of the Paris suburbs and there leading a celibate existence whose secret goings-on could not fail to scandalize his other brother, who was an abbé, and his sister, Madame d'Orbigny, who was virtuous.

Eventually I made his acquaintance. From the very first he seemed to me to be a man with whom only entomological conversation was possible. It was at a family luncheon, the first he had deigned to honor with his presence, at my uncle d'Orbigny's. Notwithstanding the excellence of the victuals and wines, and the presence of several ladies who were utter strangers to matters coleopterological, he started off, the moment the oysters were served, on an acrid and fiery criticism of his colleagues in the Entomological Society. Without any restraint he denounced the omission of a comma in a text with as much vehemence as the confusion of a species with a variety. I marvelled while he neglected the mushrooms and meat in the pâté in order to devour at his ease the honorable members of a learned Society. "Behold," said I to myself, "a man of knowledge who exalts science above friendship, above his family and even above good food. He certainly is somebody!"

Though I was greatly intimidated, I managed to screw up my courage to address him, expecting to rise in the estimation of so distinguished an uncle. I asked him about De Vries' theory of sudden mutations, which at that time had all the splendor of novelty. He glared penetratingly at me through his eye-glasses, snapped out: "Of no interest!" and continued to descant on I know not what error in Reitter's "Catalogue."

He was one of those censors of science, who, both formidable and actually feared, carry on without respite the combat against the negligence and ignorance of others. It must be admitted that the reliability and high excellence of his own works gave him a right to play this rôle. If he lacked general ideas, if the great problems of biology left him indifferent, he was none the less one of the founders of modern entomology. I leave to others more competent than myself the task of evaluating his contribution to science in the works he has bequeathed us.*



Louis Bedel (1849–1922)

* [An excellent necrology of Ernest-Marie-Louis Bedel by J. Sainte-Claire Deville is published in the ninety-first volume of the *Annales de la Société Entomologique de France* (1922, pp. 165–189). Lest some of

I wish only to speak of the man. He dwells in my memory as the type of that human species which we call the savant, a species now on the road to extinction and being replaced by the man of science, a new species represented in the bosom of the Entomological Society of France by a considerable number of specimens of excellent quality.

There are many descriptions of the savant. Every psychologist, novelist, moralist, comedy-writer, pamphleteer, fabulist, popular editor, song-writer or worldly conversationalist has evolved his own definition of this creature. Louis Bedel agreed very closely with the average type of their descriptions. If he failed to let his hair grow long, if he did not wear a redingote embroidered with the academic palms, and if he was not sufficiently absent-minded to mistake the back of a cab for a blackboard, he embodied, nevertheless, the tradition of the legendary savant in his dwelling and his mode of life.

The apartment which he occupied during the greater part of his existence, at 20 Rue de l'Odéon, was extraordinary. Not everybody who wished to, could enter it. You might pull at the bell-rope in vain; if you had not taken the pains to ask for an audience, the door remained closed. By a kind of diabolic intuition, my uncle seemed to divine the quality of the visitor from the sound of the bell and whether it announced an importunate bore or a friend. Even I, who in the early stages of our acquaintance, failed to take the precaution of announcing my visit beforehand, have many a time climbed the four flights of stairs to his domicile in vain.

If you were admitted you at once found yourself in a chaos of books and pamphlets,

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our younger entomologists infer that this investigator's ideals are no longer worthy of emulation, I have translated a few of Deville's paragraphs.

"It is somewhat presumptuous to wish to characterize in a few words the tendencies and methods of an investigator like Bedel. Nevertheless, it seems to me that he may be said, not too inaccurately, to have possessed an essentially analytic and objective mind.

"Like most intelligences of this type, he instinctively applied the famous rules of Descartes, and God knows how rigorously! All of us remember how meticulously he mounted to the sources, to the original memoirs, and verified the most insignificant note and citation. He excelled as greatly in passing from the simple to the complex, from the known to the unknown as in subdividing difficulties for the purpose of solving them and of delimiting and evaluating their component parts, till they had lost their previous obscurity and were illumined throughout.

"So far as taxonomy is concerned, he possessed in its highest perfection a sense of the hierarchy of characters. His constant preoccupation was the discovery and elucidation of the organic and essential, though often concealed, as contrasted with the superficial and fluctuating, characters. He knew how to reject, deliberately, the details of no importance which are apt to burden descriptions. How many others, possessed of the desire to be exhaustive, have succeeded only in being at the same time both diffuse and confusing!

"Though above all a describer, Bedel never lost interest in biology. In the Phytophagous Coleoptera, especially, he was always careful to summarize their development in a brief formula (food-plant, portion of plant attacked, pupation in the earth or *in situ*, period of oviposition and eclosion, etc.). His own observations on these matters have enriched science with many a previously unknown fact. Finally, thanks to the critical sense, which he possessed in a high degree, he demolished a great many legends and doubtful assumptions.

"But the most precious of his natural gifts was certainly that of knowing how to express clear ideas clearly. He excelled in persuading his readers to participate in the lucidity of his analyses. His descriptions are quite devoid of the subjective element, which is so disturbing in certain authors. On reperusing their descriptions, these authors, because they can recognize their conceptions in an improvised and faulty text, have an illusion of clarity and feel no need of improvement. Bedel, on the contrary, puts himself in the reader's place and retouches his text till it becomes, so to speak, a faithful and concise image." W. M. Wheeler.]

plunged in the darkness of what must formerly have been a reception room. The window was blocked up with all kinds of bulletins, catalogues and offprints. On the right was the former dining room metamorphosed into a library specially reserved for the science and literature of travel. Unfortunately, access to the shelves was impossible, owing to the intervening mountains of volumes, so that in order to reach Asia it was necessary first to demolish Africa. Advancing somewhat farther you came to the kitchen, where for thirty years no chicken had been browned nor any meat stew prepared. This room, too, contributed its full share to the city of books. The stove, the sink and the pantry were hidden under the *Voyage de Pallas*, the *Voyage de Bruce* and the *Collection Choisie de Voyages autour du Monde*—never had the explorers of two hemispheres felt themselves confined to such cramped quarters.

On the left the visitor discovered among other shelves groaning under the weight of entomological annals, bulletins, revues, miscellanies and catalogues, the collections of Louis Bedel themselves, housed in vast glass cases and perched on many chairs. We are now in the drawing room and it seems natural that this place of honor should be reserved for the guests of quality that streamed to the Rue de l'Odéon—I mean the Coleoptera, many of which were great personages—the "types." It was therefore impossible to find a seat, the chairs, lounges and even the humblest stool being reserved for the cartons and boxes. Passing now into the bed-room, you observed that my uncle shared it with the Chrysomelidae, the Staphylinidae, the Harpali and the Catops—all of which, since my uncle was a bachelor, was most edifying. I will add that the bed was covered with clothing and hats because the closets were also reserved for the boxes, that the writing table was swamped beneath entomological materials and printed matter of all sorts, and that my uncle, seated on the extreme edge of a chair piled with the latest numbers of the *Annales* and *Bulletins* of the Entomological Society of France, was often obliged to use his knees as a desk for the composition of a large number of his works. The only human note in this capharnaum emanated from a painting representing my grandfather at the age of fifteen—all the rest was bottles of cyanide of potassium, boxes of pins, slabs of cork, pocket-lenses, pots of glue, tweezers and labels.

Such was the setting. The man who dwelt within it was not, as I have had occasion to remark, easy to approach. He shrank from new-comers; he bristled up in the presence of phrase-makers; he growled his disapproval of the ignorant. And he had justification, for science is bound to defend itself against parasites and commensals. It was, I am sure, one of the great merits of this general honorary secretary of the Entomological Society to track down and destroy amateurishness in a department of science in which it is only too apt to establish itself.

From my tenderest years and owing to the beneficent star under which I was born, I have always loved entomology, but as I was only an amateur in this department of the natural sciences, my uncle treated me with scant affection. I could not make him appreciate the fact that the insect was leading me directly to man, and that a novelist cannot venture into the thicket of human phenomena till he has explored the infinitely more mysterious and therefore more fascinating world of animals and plants.

His brother-in-law, my uncle Henri d'Orbigny, was more naïve in his reasoning and much more urbane in his manners. He was descended, as we know, from an illustrious family, and celebrated entomology

as a religious rite; it was with him a constant obsession. Occupied with the study of the dung-beetles (Coprophagidae) and especially with that of the African Onthophagidae, of which he described several hundred new species, he worked incessantly except during three months of the year. Then he hurried to some place in the Alps, where he hiked with a kind of fanaticism, climbing hostile slopes and refractory summits till his seventieth year. He then botanized with great ardor and would have broken his neck to reach some rare species of *Gnaphalium*. This was his only infidelity to the Onthophagi.

I often accompanied him on these summer excursions. At that time I was very young and have retained an excellent recollection of my white-haired companion, whose enthusiasm and youthful impulses accorded so well with my own. He was in an ecstasy of delight at the sight of a sulphur anemone; the discovery of a rare Crassulaceous plant would make him shout till the mountains resounded with the echo of his voice. For my part, I pursued the insects, I swept and beat the vegetation and filled my bottle. On returning to the hotel I studied the collected game with my uncle. It was fascinating. Never have I known joy of just that quality during my subsequent researches on the human fauna of the European capitals. My uncle must have had a presentiment of my fate, for he could not invent enough sarcastic remarks on literature and all literary men, with the single exception of the great writer Maurice Maindron, who was forgiven much because he was also an entomologist.

At Paris it was arranged that I should dine with my uncle once a week. My aunt, who was of a talkative disposition, was permitted to entertain us during the meal with the futilities of mundane life, but as soon as the dessert and the fruit had been swallowed, we repaired to the laboratory, and it was also the rule that I should start the conversation on the new species of *Onthophagus* that had been described during the week, for my good uncle's whole life had been regulated, ordered, classified, catalogued and reduced to synoptic arrangement—his relations with his friends and family, his admirations and sympathies, his nourishment and the employment of his time.

Passionately he described the prothoracic punctuation of *Onthophagus sexcornutus* d'Orb. as "simple, fine or rather fine and rather sparse;" then that of *O. multicornis* d'Orb. as "simple, rather coarse and not dense." I could see no difference, and told him so, but he was pained, because he was proud of the minuteness and accuracy of his descriptions. Then we passed to the frontal carinae, which in the one species were "more or less short;" in the other "rather short."

"That is six of one and half a dozen of the other," said I.

"My friend," said he, "there is a shade of difference that eludes you."

I was always accused of not understanding the French language, which is extremely difficult, I admit, but I persistently denied any scientific value to such vague terms of comparison as "interstriæ provided with rather dense granules" and "interstriæ with somewhat separated granules," and this would throw my uncle into violent fits of bad humor. At bottom it really pleased him, because, though apparently very peaceful, he loved to quarrel, especially about statements. In this respect he differed from his brother-in-law, Louis Bedel, who quarreled only about men. The two brothers-in-law therefore never understood each other.

"Have you read," asked d'Orbigny, "the latest communication of X?"

"Absurd!" replied Louis Bedel.

"Why?"

"Because it is X's."

On another occasion, it was Louis Bedel, who asked:

"What do you think of Z?"

"I deny him all authority!" replied d'Orbigny.

"Why?"

"Because he is the author of such a work."

Such were my two uncles. Owing to a mental idiosyncrasy that was later to cause me much annoyance in my career as a novelist, I saw them only from the distorting angle of ironic observation. This will be evident from the perusal of the few lines which I have consecrated to them. I honestly deplore this manner of celebrating the memory of relations who were dear to me, but what am I to do? An honest writer should remain himself, especially in an apologia for members of his own family.

THE EVIDENCE FOR INHERITANCE OF RESISTANCE TO BACTERIAL DISEASES IN ANIMALS

By W. V. LAMBERT

(*Paper No. 55 from the Department of Genetics, Iowa State College, Ames, Iowa*)

THE COÖPERATION of two sets of circumstances is necessary for the development of an infectious disease. In the first place, the organism in which the morbid process is to develop must conform to certain conditions of structure and function, while secondly, an external agent, the bacterium in the case of bacterial diseases, must exert a specific effect upon the organism which is in the process of developing the disease. These facts have long been a commonplace in medical writings (see Bulloch and Greenwood (1911) for a review of the older literature), but unfortunately little attempt has been made to evaluate the rôle played by the host in disease processes. Because of the obvious need for combatting disease through control of the infective agent, most effort, naturally, has been directed toward a study of the causative agent and to the series of changes that follow its invasion of the tissues of the host. Nevertheless, the fact remains that the constitution of the host plays an important part in disease resistance, and it is probable that a more exact evaluation of this rôle will be of fundamental importance for students of epidemiology.

Much statistical and observational evidence on this problem exists, but for the most part it allows only for the general conclusion that marked differences in disease resistance do occur among animals. Attention need hardly be called to the fact that the diseases of one species are generally not pathogenic for the individuals of other species, or if so usually only to a mild degree. In many cases this resistance is so great as to be spoken of as a natural immunity.

Intra-species differences in resistance likewise exist. It is a commonly observed fact that some individuals survive severe epidemics without apparently contracting the disease, others are affected but slightly, whereas some succumb to the ravages of the disease. Many of these differences can be explained, no doubt, by environmental causes but it would be rather presumptuous to assume that all of them are due to accidents of environment.

In man, many well-founded cases of racial differences in resistance to infections have been reported. Thus, it has been pointed out by Ferguson (1928) and others, that tuberculosis is far more fatal to the peoples of uncivilized races than it is for the people of regions in which the disease has been endemic. Racial differences occur, however, in regions where tuberculosis long has been endemic. For instance, Dublin and Baker (1920) found a significantly higher death rate among the native born Irish of Pennsylvania than among the native born Italians. The difference was greater than could reasonably be explained by habits of life, differences in social or economic status or by environmental causes.

For diphtheria also racial differences in resistance occur. Holmes (1931) has pointed out that the negro is more resistant than the white man. In this case

Holmes suggested that the greater resistance might be due to a thicker ectoderm. For pneumonia likewise racial and even familial differences in resistance have been noted. Thus, Pearl (1926) has reported one family of 13 in which the incidence of pneumonia was 100 per cent, a condition which he concludes could have been in no significant degree environmental. The evidence in this case indicated that the whole family possessed a definite constitutional inferiority of the respiratory system.

In animals numerous instances of subspecific and breed differences have been observed. Tyzzer (1917) and Hagedoorn-LaBrand and Hagedoorn (1920), for example, observed marked differences in resistance among mouse stocks in their laboratories. The ordinary mouse (*Mus musculus*) was far more resistant to the infections than was the Japanese waltzing mouse (*Mus bactrianus*).

The most complete evidence of strain differences in disease resistance has been reported by Wright and Lewis (1921). In their experiments guinea pigs from five highly inbred lines were infected with tuberculosis and marked differences in resistance were found between some of these families. The high resistance of one family was transmitted alike by males and females when crossed with one of the other inbred families. In the latter crosses the F_1 progeny were superior to the resistant parent family, thus indicating the presence of complementary factors for resistance. Over 30 per cent of the variation in length of life among the crossbreds could be attributed to the amount of blood of the best inbred family.

Much other evidence of this sort might be cited but a large part of it has been reviewed by Crew (1928), by Kozelka (1929), and for man, by Holmes (1931). More recently, Darling (1932) has reviewed some of the literature and has emphasized the inadequacy and uncritical nature of much that has been written on this subject.

THE EFFECT OF SELECTIVE BREEDING ON HOST RESISTANCE

More critical evidence of the part played by the host on resistance to disease has been advanced in the last decade from laboratory experiments undertaken primarily to study this question. In most of these studies such factors as the degree of infection, route of infection, pathogenicity of the bacterium and the environment were controlled, as well as such factors as age and condition of the experimental animals. In addition, the cause of death in most instances was reasonably well established.

The investigations of Webster (1924 and 1925) were among the first to demonstrate the influence of selective breeding on host resistance. By the simple process of using only survivors of a mouse typhoid infection Webster was able to bring about a marked decrease of mortality from this disease in the course of a few generations. On the other hand, he advanced data to show that the offspring of females most susceptible to this infection produce, in turn, offspring more susceptible than a similar group of unselected mice. While the experimental data were too few to allow for sweeping conclusions, Webster's experiments had the merit of being carried on in such a manner as to reduce to a minimum the possibility of a specific acquired immunity.

A more critical investigation of the genetic basis for resistance to mouse typhoid was conducted by Schott (1932). In his experiments the breeding mice not only were survivors of a standard infection with the causative bacterium, but they came from those families showing the highest progeny resistance. As a result of

six generations of such selective breeding the mortality in the selected stock was reduced to 24 per cent, whereas the foundation stock from which the selected population descended showed a consistent mortality of over 80 per cent. A control (unselected) population, consisting of 538 animals of the same strain as the selected stock, that were tested at intervals throughout the six generations, showed 82 per cent mortality. Rate of mortality as well as total mortality was decreased by selection. The matings in this experiment were so directed as to concentrate the blood of those individuals giving the highest progeny resistance, and it was found that a large part of the high resistance of the selected population could be traced to the influence of a few "key" animals.

Hetzer (Unpublished data) has continued this investigation and finds that selection is still effective within this stock, but the increase in resistance has been at a rather slow rate, a situation that also was observed by Schott in the later generations. It is probable that the end point of selection in this stock has nearly been reached, for the degree of inbreeding within the selected stock is now very high. Hetzer has increased the standard infection fourfold in the last generation with a resultant increase of approximately 9 per cent in mortality. This fact would indicate that there is a rather delicate balance between those innate factors for resistance and such environmental factors as degree of infection.

Using a similar plan of selection Irwin (1929) was able to increase the resistance of the rat to a standard infection with the Danysz bacillus (*Salmonella enteritidis*). Three generations of selection resulted in a decrease in mortality from 85 to 35 per cent. In this experiment, as in those of Webster and Schott, the greatest effect of selection was observed in the first generation.

Similar experiments conducted in chickens by Roberts and Card (1926) using *pullorum* infection and by Lambert and Knox (1928) for resistance to fowl typhoid have given quite similar results to those reported above. Recently, Roberts (1932) stated that the strain of fowls selected for resistance to *pullorum* infection was much more resistant than fowls of the unselected population that were so infected, the respective mortalities being approximately 35 and 73 per cent. These differences have been reasonably consistent for seven consecutive generations. His investigations, furthermore, have shown that chicks from some matings are far more resistant than those from other matings and that these differences are very consistent. Lambert (1932a) has been able to reduce the mortality from fowl typhoid from 85 per cent to 10 per cent as a result of five generations of selective breeding. Since much variability was observed for different matings in the resistant stock in the latter experiment, even after five generations of rigid selective breeding, it would appear that considerable genetic variability still existed in this stock.

Recently, Manresa (1932) has shown that marked inherent differences in resistance exist in rabbits to infection with *Brucella abortus*. He was able to differentiate rabbits into reasonably true breeding susceptible and resistant lines by a program of careful breeding based upon the female's reaction to an injection of virulent *B. abortus* bacteria. In this study the criterion of resistance was the ability of a doe to bring to full term a litter of normal young rabbits following an intraperitoneal injection of the bacteria near the fourteenth day of pregnancy.

Frateur (1924) proposed a mono-factorial difference as controlling resistance

and susceptibility to fowl diphtheria, but his data are so few that this conclusion can be considered as no more than suggestive. Topley (1926) as a result of his extensive studies on the epidemiology of mouse typhoid clearly recognizes the importance of the hereditary element in disease resistance, for he states that a colony may increase its average resistance by a process of simple selection; namely, by the elimination through death of the more susceptible members.

CAN A PASSIVE TRANSFER OF IMMUNITY BE PRIMARILY RESPONSIBLE FOR THE INCREASED RESISTANCE IN THE SELECTED STOCKS?

The experiments just cited prove that selective breeding is decidedly effective in increasing resistance to a given disease but it may be suggested that other factors could be responsible for some of this increased resistance, such as a passive transfer of resistance from the dam to her progeny. If this were true, then only a part of the increased resistance could be genetic in origin. While the continued effectiveness of selection over a number of generations would seem to refute this possibility, experimental data are at hand which show that a passive transfer of immunity cannot have played a major rôle in the increased resistance of the selected stocks.

In order to test the possible influence of this factor upon the resistance of selected offspring Schott (1932), Lambert and Knox (1929) and others early in their experiments made two series of matings to test this question. One series consisted of selected males by unselected females while the second series consisted of the reciprocal matings. The data from these experiments indicate that the male transmits resistance to the progeny in nearly equal degree with the female. Since Smith (1907) and others have shown that passive immunity is not transmitted through the sire it would appear that a passive transfer of immunity cannot have been responsible for the increased resistance of the selected stock.

Further evidence on this question has been advanced by Roberts and Card (1926) and by Lambert (1932b), who have shown that the progeny from surviving carrier hens are no more resistant than chicks from non-carrier hens. Again, the fact observed in their experiments that some pairs of birds produce far more resistant offspring than do other pairs of birds provides additional negative evidence against a major influence of the passive transfer of immunity.

Regarding the development of an active immunity previous to the time of receiving the test dose, the evidence is again largely negative, though in some cases this factor may have played a part in enhancing the resistance of the selected stock. Had it been a major factor, however, it would have been expected that the effectiveness of selection would have been reached in the first or second generations. As previously shown, this was not true. In the case of the experiments of Roberts and Card (1926) this criticism cannot be made for the chicks were inoculated when one day old and hence could not possibly have acquired such an active immunity. While it is true that some eggs produced by carrier hens do transmit the infection, the proportion of such eggs on the whole is small (see Weaver and Weldin, 1931), and thus in no sense could this factor have had a major part in bringing about a greater resistance of the selected stocks in these experiments. The experiments of Lambert (1932) furnish additional negative evidence of this sort.

The experiments of Webster, as previously mentioned, were conducted to reduce the possibility of such preinoculation infection to a minimum, so it could

not have been an important factor in his experiments. Manresa found that females produced by actively immunized susceptible does were no more resistant than were the females produced from non-immunized susceptible does. Furthermore his experiments were so conducted as to rule out either the passive transfer of immunity or an active immunity acquired by sublethal infection previous to the time all females were submitted to test.

The most convincing evidence on this point has been obtained by Gowen and Schott (unpublished data kindly furnished to the writer). Susceptible females of an inbred strain of mice were double mated to susceptible males of their own strain and to resistant males. The matings were made so that the offspring from the different males could be determined from the color of the offspring. From the susceptible males 20 offspring were produced all of which died when submitted to the standard infection of mouse typhoid bacteria. From the resistant males 15 offspring were produced and tested. Of this group only 8 died. While the data are few, this experiment clearly demonstrates the importance of genetic factors for resistance and shows, furthermore, that they are transmitted by the sire to his progeny.

In the face of all of this negative evidence it would seem justifiable to assume that a passive transfer of immunity, or the acquisition of an active immunity in the young stock, acquired by sublethal infection before test, have not played a major, if any, rôle in the increased resistance of the selected stocks used in the above experiments.

THE GENETIC NATURE OF RESISTANCE AND SUSCEPTIBILITY

A genetic analysis of resistance and susceptibility to disease in animals presents many difficulties not encountered in the analysis of other characters. In the first place it is very difficult in most cases to establish clear-cut classes of resistant and susceptible animals. While the classification of dead or alive may be used, obviously such a classification does not take into account the various sublethal infections in the surviving population. Secondly, such a character as disease resistance is influenced markedly by environmental factors, some of which are very difficult to control. Finally, since disease in the sense used in this paper is a manifestation of the growth of an infectious agent in the tissues of the host, a variable is introduced which is not encountered in most genetic analyses. Obviously, therefore, it is mandatory in such studies that all external conditions, as virulence of the bacterium, degree of infection, and environment, must be controlled insofar as control is possible.

In spite of these obstacles, however, some facts have been presented that bear on this problem. From the mortality observed in stocks of ordinary mice, in Japanese waltzing mice and in their F_1 and F_2 hybrids, Hagedoorn-LaBrand and Hagedoorn (1920) suggested that the inheritance of resistance and susceptibility probably depended upon a monogenic difference. In this investigation the pathogen was not determined, nor was the degree of infection controlled, the mortality resulting from a spontaneous epidemic in their colony.

Frateur (1924), as previously mentioned, proposed a monogenic difference between resistance and susceptibility to fowl diphtheria, but the data are too few to be more than suggestive that this simple explanation is correct. Rosling (1929), from the results of reaction to the Schick test for diphtheria in 97 Copenhagen families, suggested that the rate of antitoxin production is governed by one pair of genes, individuals of the recessive type having

only a limited ability to produce antitoxin. The data of the Hirszfelds (1927) would not agree with such a simple interpretation.

Irwin (1929) crossed susceptible rats of an inbred strain with the first selected generation animals of a selected strain resistant to the Danysz bacillus. The F_1 individuals possessed an intermediate degree of resistance. F_1 individuals were crossed inter se and also back to animals of the susceptible strain. In the backcross generation stock about 50 per cent mortality occurred, whereas only 25 per cent mortality was observed in the F_2 generation. While these results might suggest a monofactorial difference between resistance and susceptibility, Irwin concluded that resistance was due to a complex of hereditary factors some of which are partially dominant. Similar conclusions were reached by Schott (1932) in regard to resistance to mouse typhoid and by Lambert (1932a) for fowl typhoid.

Roberts (1932) crossed chickens of a selected *pullorum* resistant strain with unselected birds, then crossed the F_1 birds to both the resistant P_1 and the unselected P_1. The F_1 generation was about as resistant as the P_1 resistant strain, showing only about 35 per cent mortality; the backcross generation from the cross of F_1 birds to the resistant P_1 showed a mortality of 37 per cent while the offspring from the F_1 by unselected P_1 gave a mortality of 62 per cent. In addition, F_1 birds were mated inter se. The F_2 progeny from these crosses showed a range from low to high resistance. Selections of breeding stock were made from the classes showing both low and high resistance in the F_2 generation. The offspring from the high segregates that were tested in 1931 showed a mortality of 31 per cent, while the mortality in the chicks from the low segregates gave a mortality of 92 per cent. These results show clearly the importance of genetic factors for resistance but do not permit of an exact estimate of the number of factors concerned.

Manresa (1932) tentatively concluded that the inheritance of resistance and susceptibility to infectious abortion in rabbits is governed by one pair of Mendelian genes and that resistance is dominant or partially dominant. Some objections were encountered to such a simple interpretation, however, and it is probable that more extensive tests will show the genetic basis of resistance and susceptibility in this case to be more complex than a monogenic difference.

In plants the genetic analysis of resistance and susceptibility to disease has been carried much farther than in animals (see Hayes, 1930, and others). Where a genetic analysis has been made in plants it has been mostly in self-fertilized species or in strains where, by long self-fertilization, a high degree of genetic purity or homozygosity has been attained. The use of such homozygous resistant and susceptible strains has made possible a clean-cut genetic analysis of disease resistance in some cases, as well as having furnished critical evidence on the physiological interrelations between host and pathogen.

In animals few highly inbred strains exist, and in those that do exist it is improbable that highly resistant lines will be found, since no selection for resistance was practiced during the development of such strains. Because of the complexities introduced by environmental causes and the interrelations of host and pathogen, it would seem that a careful genetic analysis of resistance and susceptibility to any disease must await the development of inbred lines which will react in a uniform and constant manner to infection with a given pathogen. Much progress, of course, may be made in the development of resistant strains without a genetic analysis, but a complete knowledge of the

part played by the host in disease processes will probably await a genetic analysis.

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ON THE GENETIC STRUCTURE OF INHERITED CONSTITUTION FOR DISEASE RESISTANCE

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IT IS a familiar fact that even after repeated exposure to a disease there are some animals which will show no history of having had this disease. These refractory animals are, in common parlance, said to have a good constitution. In the literature on animal diseases it is frequently asserted that this good constitution for one disease is also apt to presage like resistance to another disease or unfavorable lethal entity of a quite different nature. In other words constitution is held to be a single unit type of character which enables the animal to resist a multiplicity of environmental agents. This concept has been built up largely around observation on animal diseases.

This view is opposed by the extensive experiments and observations which have been made on disease resistance in plants. These studies have almost uniformly led to the conclusion that genetic constitution for disease is a composite made up of numerous genetic factors, some making for resistance to one disease and some to another, the fortuitous combination of these factors leading to resistance to both.

The study of genetic factors which cause obvious pathological constitutional defects or death is also opposed to this view. A striking illustration of this fact is the case of a lethal factor which causes melanotic lesions of the leg joints in *Drosophila*. These lesions incapacitate the fly, causing its death. The inherited predisposition to this condition is specific, being dependent on a single inherited gene. This gene is entirely distinct from the 350 other genes which produced the other constitutional changes studied in the same experimehts (1). Another equally striking case is that described by Mohr and Wriedt (2) in the Swedish breed of Holstein-Friesian cattle. In the homozygous condition one of these lethals produces congenital hairlessness accompanied with death, while the other causes the amputation of all prominent parts. The lethal factors causing these defects in the animal's constitution are widely distributed within this breed, due to the fact that two very prominent imported sires of excellent individual appearance were heterozygous for one of the pathological conditions, one for hairlessness, and the other for amputated extremities.

It is obvious that a marked and fundamental difference of interpretation exists between those who have studied animal diseases of bacterial origin and those who have studied plant disease of like origin or those studying pathology of either plant or animal of genetic inception. The question arises how are these two views to be harmonized.

The words specific and non-specific factors for disease resistance have been frequently used in discussion of this subject. These words have unfortunately different meanings in the two overlapping

sciences into which disease resistance studies naturally fall. In the immunological sense specific factors for disease resistance are taken to mean factors which cause resistance to one and only one disease, however closely related to it a second disease may be. In a still more restricted sense specific factors are sometimes thought of as identical with the immune bodies which the animal body forms after an attack of the disease and which are known to be quite specific for the given bacterial agent causing it. In this sense non-specific factors are defined as attributes which cause resistance to many agents. Genetic terminology of long standing has given these terms a quite different meaning. Specific factors have long been defined and thought of in terms of genes carried in the germ plasm. They are the inherited entities which guide body development to the formation of special characters. One of these factors may make for resistance to one or several lethal agents. Since this resistance is dependent upon one factor this factor is regarded as specific for it even though the developmental expression of it may have multiple effects. Non-specific factors are regarded more as variables of the environment, temperature, food available to the animal, etc. In this paper the genetic usage will be followed.

Genetic constitution could conceivably be either a single character which enabled the organism to resist a multiplicity of environmental agents or a composite of numerous independent characters each of which is capable of causing the individual to resist one environmental agent, the fortuitous combination of these separate characters making animals resistant to many or few such agents. The implications which follow in the wake of these two hypotheses are markedly different. If constitution were a single character its inheritance would be expected to be simple. If on the other hand it were a composite of many individual characters then its inheritance need not be simple. The consequences of epidemic disease and their bearing on future epidemic diseases within a herd composed of individuals made up according to the first hypothetical constitution are very different from those in a herd composed of individuals with the second hypothetical constitution.

RESISTANCE IN MICE

The study of the genetic structure of constitution may perhaps best be approached by differentiating relatively pure and distinct lines within a species by matings designed to separate genetically distinct lines and then studying these groups exhaustively from the viewpoint of their reaction to agents chosen because they are believed to be distinctly different. For some years the work of our laboratory has been directed toward this problem. Among the genetic strains which we have collected and studied in these experiments were two which proved to be differentiated in their disease reactions. Throughout this work the writer has been associated with Dr. Ralph G. Schott.

The two lines S and sil were shown in the previous experiments to be distinct in their reactions to the pseudorabies virus. The S strain in a population of 190 showed the low survival rate of only 8.4 ± 1.4 per cent to this disease. The sil strain in the same experiment had a much higher survival, this rate being 52.2 ± 2.5 per cent in a population of 176. The F_1 hybrids' rate of survival was 23.7 ± 3.7 per cent in a population of 59. Many of those surviving the inoculation of the pseudorabies showed no symptoms of the disease, except that they became immune to a subsequent inoculation of a much larger

amount of the virus which would otherwise have been surely lethal.

On the basis of survival, the sil stock would be considered much superior to the S stock. If constitution is a general over-all single character in inheritance the sil stock would be expected to show a higher survival value for any other pathological agent. If on the other hand constitution is made up like other general somatic characters, composed of many separately inherited entities, the sil stock would not be expected to show higher survival value for other pathological agents.

It is possible to test this question since these two lines had previously been differentiated on the basis of their resistance to mouse typhoid, *Salmonella aertrycke* by his colleague R. G. Schott, Genetics 17: 203. The S line when inoculated with a standard dose of 5×10^4 organisms had 75.3 per cent of its individuals survive. The sil strain on the other hand had no mouse survive this dose. Crosses between these lines showed that the resistance of the S line was transmitted through both males and females. The survival rate of the F_1 crosses was 62.6 per cent. The typhoid disease behaved differently from the pseudorabies disease in the fact that all animals inoculated showed distinct symptoms of the disease. None escaped showing some traces of its effect. A test through the use of double matings has shown these differences to be genetic in origin.

The significance of these differences may be tested by their χ^2 values. In the pseudorabies experiments there were 190 mice of the S line tested, 174 of which died and 16 survived. In the same experiment the sil strain had 176 mice tested, 84 of which died and 92 survived. The F_1 cross between the S and sil lines had 59 progeny of which 45 died in test and 14 survived. In the previous generations the test for the survival value of these three groups to an inoculation of a standard dose of *Salmonella aertrycke* organisms showed that of 105 tested in the S line 26 died and 79 lived; of 108 individuals tested in the sil line all died; and of 187 F_1's tested 70 died and 117 survived. The χ^2 and P values for the different combinations are shown in table 1.

TABLE 1

	CLASSES COMPARED	χ^2	P
Pseudorabies	S with sil	84.5	<0.001
	S with F_1 (S × sil)	10.0	0.002
	sil with F_1 (S × sil)	14.5	<0.001
Pseudorabies rates compared with *Salmonella aertrycke* rates		225.6	<0.001
Salmonella aertrycke	S with sil	30.5	<0.001
	S with F_1 (S × sil)	38.5	<0.001
	sil with F_1 (S × sil)	110.8	<0.001

The survivorship curves shown in figure 1 bear out the same interpretation. The solid line represents the per cent of the sil strain surviving plotted against days after inoculation. The dot and dash line shows the same information for the S strain. The F_1 hybrids survivorship curves

are represented by the dotted lines. The plots are made on the same logarithmic scale so that equal rates are visible to the eye. The pseudorabies graph is quite distinct from that of the mouse typhoid in a number of particulars. There is first a definite incubation period. When deaths commence on the third day the survival line falls in very nearly straight lines from the initial origin of 100 per cent living animals throughout the cycle of the disease, when deaths cease nearly as sharply as they began. The cycle of the disease consists of only 3 day incubation period and 6 days when deaths are taking place. It will be noted that the S animals die at a much faster rate than the sil strain. The F_1 rate is approximately intermediate between the two parental strains.

The mouse typhoid curves present a markedly different picture. Deaths commence on the second day with a slow but constantly increasing rate. The sil and the S strain have now reversed their rates of death from those seen in the pseudorabies disease. All of the sil animals die off rapidly, the survivorship curve reaching zero on the fourteenth day. The S strain shows a slow rate of death and a high final survival value. The F_1 hybrids show somewhat less survival than the S parents and a markedly greater survival than the sil stock. The duration of the disease is distinctly longer with the mouse typhoid than with the pseudorabies with all strains.

These data show that the two lines of mice, S and sil, are distinctly different in their reactions to pseudorabies virus on the one hand and mouse typhoid organism, *Salmonella aertrycke*, on the other. The fundamental basis of these differences has been shown to be the genetic constitutions of these two strains. A genetic complex which is favorable to the survival of a strain when exposed to one pathological agent is here shown to favor susceptibility to another agent. The hybrids react like the S parents, showing a marked difference in dominance of the genes comprising the constitutions of these two lines. The genetic constitution for resistance or susceptibility to these diseases is shown by the data to be a composite of separate genes each capable of causing the individual to

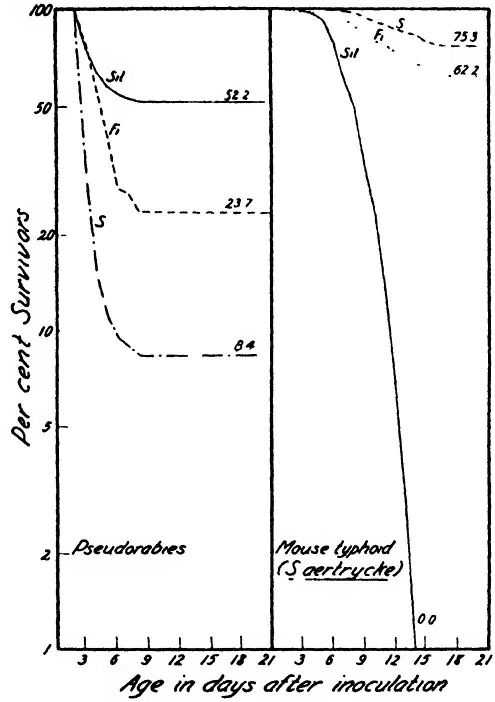

Fig. 1. Survivorship Curves of the S and sil Strain and Their F_1 Hybrids for Pseudorabies and Mouse Typhoid

resist one environmental agent. The fortuitous combination of these separate factors makes animals resistant to many or few such agents.

These two lines of mice are simply two strains which have been differentiated genetically by breeding. A random bred stock would very probably contain both types well mixed within it. In point of fact in obtaining stocks from three different dealers in mice we obtained results

which would be called for by such a mixture. They exhibited the full range of variability which was found in the combined results from our resistant and susceptible lines.

The significance of these results to our problem is quite obvious. So far as this population, composed of these two strains, is concerned its resistance to these two diseases is on a distinctly different genetic basis. Selection for resistance to one of these diseases within this herd would result in susceptibility, not resistance, to the other. A constitution favoring resistance to both of these diseases simultaneously would be a fortuitous combination of the genetic resistances of both strains unless it were true that the genetic factors for resistance to one agent definitely produced susceptibility to the other.

RESISTANCE IN OTHER ANIMALS

Other work in the animal field has in part been interpreted as supporting this view of the composite nature of genetic constitution and in part that constitution was a single character. Lambert (3) has established a strain of White Leghorns which are resistant to the fowl typhoid bacterium, *Salmonella gallinarum*. Roberts (4) has established a strain of white Plymouth Rocks resistant to white diarrhea, *Salmonella pullorum*. Lambert (5) made tests of both strains for their cross resistance. Ninety-seven of the white leghorn strain resistant to fowl typhoid were tested for their resistance to *Salmonella pullorum*. Fifty-five per cent of the birds died on this test whereas for a like number of controls 86 per cent died. The generation of selection from which these resistant birds came had a death rate of slightly more than 15 per cent when inoculated with *Salmonella gallinarum*. Fifty-five of the White Plymouth Rocks resistant to *Salmonella pullorum* were inoculated with a standard dose of *Salmonella gallinarum*, with the result that 78 per cent died. The control group of 48 birds showed a death rate of 83 per cent.

The results for the birds which were initially selected for resistance to *Salmonella gallinarum* and subsequently were tested with *Salmonella pullorum* can be interpreted in at least two ways. (1) Resistance may be looked upon as due to a unit rather than a composite constitution, in which case the increased resistance to *Salmonella pullorum*, brought about by selection of resistance to *Salmonella gallinarum*, would be due to non-specific factors. Since, however, the resistance is not as complete with *Salmonella pullorum* as it was with *Salmonella gallinarum* it follows that the genetic basis of constitution must still be quite largely due to multiple separate factors or be composite. Or (2) since *Salmonella gallinarum* is closely related to *Salmonella pullorum* in a taxonomic sense it would be likely to have some like methods of producing disease as well as some unlike ones. The selection for resistance would consequently select for resistance to these like methods which would in turn give the selected stock a better chance of survival than the control stock lacking the genetic constitution for this resistance. The case could consequently be interpreted as indicating that constitution is a composite of numerous independent characters.

The data for the *Salmonella pullorum* resistant race cannot be interpreted as due to non-specific factors since the selected and control strains have no significant differences in their death rates. Differences in the technique of exposing the strains to disease might have a direct bearing on the problem in hand, however. Roberts selected for disease resistance by feeding his birds the standard dose by mouth. Lambert tested the resistant strain developed

by this mouth feeding by intraperitoneal inoculation, a different route. This factor, the difference in the body cells which would be called upon to resist the initial attacks of the organisms, could conceivably account for the fact that the birds selected for this one type of resistance showed but little resistance when another type of unselected cells were exposed to attack. Lambert has tested this question, however, and finds that the route of infection makes little difference in the survival rates when the doses are within the range used in the experiments.

Webster (6, 7) has studied the question of constitutional resistance from several different viewpoints. In one experiment mice which had survived a single but varied dose of five different organisms: mouse typhoid I; mouse typhoid II, *B. aertrycke*, *B. pestis caviae* and *B. paratyphosus B*; were injected by stomach tube with a standard dose of epidemic mouse typhoid strain II. The results of this experiment showed the survival value of the previously unexposed mice to be the least, 20 per cent; those mice previously exposed to bacilli of low pathogenicity, *B. pestis caviae* and *B. paratyphosus B.* next, 48 per cent surviving. The groups of mice exposed to bacilli of moderate pathogenicity, mouse typhoid II and *B. aertrycke* showed a still higher survival rate, 69 per cent and 73 per cent; the mice surviving bacilli of highest pathogenicity, mouse typhoid I, a survival rate of about the same value as that for mice surviving the attacks of moderately pathogenic organisms, 67 per cent. The order of this resistance for the different groups to the mouse typhoid II disease follows that of the pathogenicity of the previous organisms to which the mice were exposed rather than the agglutination relationship of these different bacterial species. From this fact Webster draws the conclusion that the resistance mechanism of the host contains important non-specific factors. From the viewpoint of immunology, as indicated earlier in this paper, this conclusion appears to be correct. It should not be carried over to the genetic concept of the host resistance to disease, however. The variations in the survival rates to the second inoculation seem to support, rather than otherwise, the view that the resistance in even such closely related diseases as those here studied is dependent upon quite specific genetic factors.

RESISTANCE IN MAN

Other observations on variations in racial susceptibility to two or more injurious environmental agents seem to be confined to statistical studies of death rates of peoples of various racial groups. Dublin and Baker (8) have made one of the most extensive of these in their study of mortality of race stocks in the states of Pennsylvania and New York. Their data are presented in the form of age specific death rates from five groups of diseases, tuberculosis, cancer, organic diseases, pneumonia and Bright's disease. The death rates in these states of peoples derived by immigration from six different racial stocks, Irish, German, British, Austro-Hungarian, Italian and Russian are presented. The general sense of their findings, although not the specific differences, may be indicated by arranging the racial groups in order of their death rates, from those having the highest to those having the lowest, for each disease (table 2).

While it may be argued that the division into the different racial groups, Irish, German, etc., can be regarded as not more than an approximation to the genetic homogeneity of animals bred purposely for uniformity, the data distinctly argue for racial differences in susceptibility to these diseases. These racial differences

extend to more than one disease, in fact in the racial groups Irish, German and British they extend to all five diseases. It is this type of data which some have interpreted as indicating that genetic constitution for disease resistance may be rather simple, possibly a unit, in its factorial composition. Such a conclusion appears somewhat premature. A good deal of necessary evidence is yet to be gathered to establish such a view, i.e. it would at least require crossing of the racial groups and a study of the hybrids. The data as they stand are furthermore equally capable of having the disease resistance of the different races interpreted as due to the fortuitous combination of several genetic factors, one contributing resistance or susceptibility to one disease and another to another.

TABLE 2

TUBERCULOSIS	CANCER	ORGANIC DISEASES	PNEUMONIA	BRIGHT'S DISEASE
Irish	Irish	Irish	Irish	Irish
German	German	German	German	German
British	British	British	British	British
Austro-Hungarian	Russian	Russian	Italian	Austro-Hungarian
Italian	Austro-Hungarian	Austro-Hungarian	Austro-Hungarian	Russian
Russian	Italian	Italian	Russian	Italian

RESISTANCE IN PLANTS

The studies on plant diseases of bacterial and fungous origin also lead to the view that genetic constitution for disease resistance is of the multiple specific factor type. The degree of genetic complexity manifested by the given host disease relationship varies greatly depending both on the host and on the disease. Only briefest mention of the extensive data in this field can be made. One of the simplest host-disease relationship is that of fusarium wilt of cabbage studied by Walker (9). Resistance to the wilt was apparently due to a single major factor, resistance being dominant to susceptibility. This disease resistant factor was independent of other factors which made for resistance to other environmental agents. The case is much like the *piliformis* disease of mice which the writer has been studying. Here strain susceptibility is quite sharp and the major factor for resistance behaves as a dominant independent of several other resistance factors.

Resistance to anthracnose in the bean plant has been shown by McRostie (10) to be equally dependent on the genetic composition of the bean host and the anthracnose organism, *Colletotrichum lindenuthianum*. The alpha strain of anthracnose infects only plants homozygous for the recessive alpha gene. The beta strain of anthracnose infects only plants homozygous for another recessive gene. It takes the combination of these two genes in homozygous condition to make the plant susceptible to both strains. The two genes are independent in their inheritance. This particular disease and host relationship has been further extended by Burkholder (11), who isolated still another strain, gamma, of the anthracnose producing *C. lindenuthianum*. Host resistance to this strain is likewise dependent on a single mendelian factor. The variety of bean, Well's Red Kidney, which was resistant to both the alpha and beta types of *C. lindenuthianum* is susceptible to the gamma type.

Although the common rule seems to make factors for resistance dominant to

those for susceptibility this is not always the case. Dietz (12) working on rust resistance in oats showed that susceptibility to the rust infection in a cross between the varieties white Russian and Burt was dominant, the resistance being dependent on two factors, one of which inhibited the expression of the factor for resistance carried by the white Russian parent.

As with the animal disease studies, the reactions of different varieties of plants within a species may be classified into three broad categories: the plant may be naturally immune to the disease, showing no reaction on exposure to it; it may be resistant; or it may be susceptible, offering little opposition to the progress of the infection. Aamodt (13), studying the genetics of a strain of wheat, Kanred, immune to rust form 1, a strain which showed lesions of the disease but resisted its further encroachment, Kota, and a susceptible strain, Marquis, came to the conclusion that this difference in the reaction was due to three allelomorphic factors. Immunity was dominant to the resistant and susceptible allelomorphs.

Immunity or resistance to several physiologic forms of rust may be conferred by a single gene or it may limit itself to one form. This overlapping of the gene effects on physiologic forms of rusts may be such as to preclude combination of the resistance of one variety to different physiologic forms of rust with that of another variety to the physiologic forms to which it is resistant, one allelomorph of the pair making for resistance to one group of diseases and the other allelomorph making for resistance to another group of diseases. Such a case has been noted by Goulden, Neatby and Welsh (14). Their study of the reactions of the wheat varieties H-44-24 and Marquis lead them to conclude that variety H-44-24 was relatively resistant to rust forms 9, 14, 17, 21, and 34 but somewhat susceptible to 15. Marquis on the other hand was resistant to rust 14 and susceptible to 9, 15, 17, 21, and 34. These differences are held to be dependent on a single factor pair, the H-44-24 being homozygous for the RR resistant factor and the Marquis for the rr susceptibility allelomorphs. If this is true it then becomes impossible in this cross to combine the moderate resistance of the H-44-24 to rust form 21 with the high resistance of Marquis to rust form 14.

In oats the variety Victory has been shown by Gordon and Bailey (15) to be susceptible to six forms of the stem rusts. White Russian is resistant to forms 1, 2 and 5 but susceptible to 3, 4 and 6. Richland is resistant to forms 1, 2, 3 and 5 but susceptible to 4 and 6, while a selected strain of Joanette is resistant to 1, 3, 4, 5 but susceptible to 6. Definite differences in the genetic constitutions of the host are responsible for these differences. Attaining resistance to one form of rust by selection may evidently lead to susceptibility, not resistance, to another.

The same conclusion is to be derived from an examination of diseases less closely related than the physiologic forms of the rusts (Hayes, 16). Wheat has as serious diseases stem rusts, leaf rust, scab, bunt or stinking smut, loose smut and black chaff. Ceres, a selection from Kota Marquis, is resistant to stem rusts but is somewhat susceptible to leaf rust, bunt, loose smut and black chaff. Marquillo, a selection from Iumillo with Marquis, is resistant to stem rusts and somewhat resistant to leaf rust, black chaff and bunt, but susceptible to root rots. Certain selections from Eimer by Marquis crosses are resistant to stem rust, leaf rusts, bunt and loose smut but are susceptible to black chaff. These facts demonstrate the specific nature of genetic resistance in the host.

It is possible to turn the case around and say that the genetic constitution of the invading organism is the significant fact in

disease resistance. That the specific genetic composition of the disease producing organism is one of the variables in disease production has already been seen in the work of McRostie and Burkholder. It is equally strikingly demonstrated by the stem rust of wheat and oats as shown by Stakman (17) and his co-workers where numerous separable and stable physiologic forms have been distinguished. Attempts to alter these forms by outside agencies or to show them unstable have thus far failed. Their genetic constitution seems to maintain and to prescribe the limits of their pathogenic powers. If new forms arise they appear to arise as mutations of the same rare frequency as mutations in higher forms or to be the product of segregation of previously existing factors through hybridization and subsequent recombination as shown by the work of Newton and Johnson (18) and Caigie (19).

While the evidence here chosen for presentation is necessarily selected, as its volume precludes presenting it in full, it is believed to be a random sample of the available data. The data show the genetic constitution of the host to be a primary variable in the disease syndrome. The genetic organization of the pathogen has like importance. Evidently the genetic constitutions of both must properly fit together for the pathogen to invade the host and produce the characteristic clinical picture of the given disease. The comparison of the susceptibility of a population to two or more diseases shows that in the majority of critical cases the genetic constitution of the host is a composite of numerous independent factors some favoring resistance to one environmental agent and some to another, the fortuitous combination of these separate factors making the organism resistant to many or few such agents.

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POLYEMBRYONY IN THE ARMADILLO: GENETIC OR PHYSIOLOGICAL?

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THE PROBLEM

THE nine-banded armadillo, *Dasypus (Tatusia) novemcinctus*, is of special interest to biologists, since it and the closely related *D. hybridus* are the only vertebrates which are known to exhibit specific polyembryony; i.e., in which the fertilized ovum regularly gives rise to more than a single embryo. Von Jhering pointed out, in 1885, that the females of hybridus gave birth to several young of the same sex, and surmised that they came from a single egg. In 1909 this supposition was given definite proof by Fernandez, and in the same year Newman and Patterson published a notice showing the occurrence of a similar phenomenon in novemcinctus. Patterson followed this in 1913 with a detailed account of the embryology (of novemcinctus) from the stage of the monodermic blastocyst through the origin and organization of the four embryonic primordia. In this paper Patterson noted his discovery of a delay in the implantation of the blastocyst, and stated that this quiescent period during which the vesicle lay free in the uterine cavity lasted at least three weeks. This statement was seized upon by other workers and was made the basis for a "physiological" theory of the cause of twinning, a theory whose superficial plausibility has largely camouflaged its vital deficiencies and contradictions. Briefly put, this theory is to the effect that the delay in development directly causes the twinning.

In a recent paper the writer has described the complete reproductive cycle of the Texas armadillo, *D. novemcinctus texanus*. The length of the quiescent period was found to be about fourteen weeks. This "free vesicle" stage was made the object of special study with the idea of evaluating the factors that were supposed to cause polyembryony. Some of the facts brought out by this investigation, the details of the budding of the embryonic primordia as described in Patterson's original paper, and certain work done on other mammals have all combined to cast strong doubt upon the validity of the physiological explanation for polyembryony, at least insofar as the armadillo is concerned, and to suggest that the time is opportune for a critical scrutiny of this theory and for an attempt to arrive at a rational explanation of twinning.

THE NEWMAN-STOCKARD THEORY

The occurrence in the same animal of a quiescent period in its embryology and of a constant form of polyembryonic development is a coincidence that could not fail to attract attention, and it is inevitable that the question should be raised as to the possible causal relationship between the two phenomena. The first published suggestion that polyembryony in the armadillo may be caused by interrupted development is found in Newman's *Biology of*

Twins. Newman suggested that the slowing down of development permitted secondary centers of growth to arise, these forming the primary and secondary buds which give rise to the embryo.

Stockard, in 1921, carried the theory forward another step by attributing the "loss of dominance" of the original axiation to a deficiency in the oxygen supply during the free vesicle period. Stockard's theory, reduced to its essentials, is as follows: The ovum of the armadillo lies free in the uterine cavity for some weeks during which time the lack of connection with the uterine mucosa brings about a deficiency of available oxygen. This lack of oxygen suppresses the original growing point on the blastoderm and allows new centers of proliferation to arise. When implantation finally occurs, the oxygen supplied allows development to be resumed; and the secondary growing points each form a primitive streak and, eventually, an embryo. Stockard was led to suggest a lack of oxygen as the causal factor from his experiments with Fundulus, in which a small number of double monsters were found when eggs were exposed to cold or crowded during their development.

The theory of discontinuous development as the causal factor of polyembryony was further elaborated by Newman in his *Physiology of Twinning*. Newman, although he criticizes vigorously certain points in Stockard's theory, adopts the latter almost without change. The principal difference between the two theories seems to be one of language rather than of thought. Newman not only restates the hypothesis that the delay in development is the cause of twinning, but he attempts to extend the theory to explain twinning in groups as alien to each other as the echinoderms, annulates, and vertebrates. We are concerned here with the theory only as it affects the armadillo, and I shall review only the part which bears on this animal.

The larger part of Newman's chapter on the armadillo is taken up by his discussion of "fission" versus "budding" as the means of separation of the embryonic primordia. This terminological skirmish seems rather pointless as it can have no possible bearing upon the cause of polyembryony. It should be said, furthermore, that the assumption on which Newman bases this whole argument is false. He objects to the term "budding" on the grounds that there is no common stock from which budding could take place; while, as a matter of fact, the common amniotic vesicle from which the embryonic primordia bud off is not only much larger than the buds, at the time they arise, but is actually larger than all four diverticula combined (see Patterson, 1913).

Newman places the immediate cause of twinning as a "partial loss of polarity or deaxiation" followed by "the physiological isolation of two, then four, growing regions" and the "independent development from the four growing points of four complete embryos," an idea which is essentially that expressed by Stockard. The conditions which bring about this supposed "physiological isolation" are a lack of "food and oxygen and a means of eliminating waste;" a lack which follows the failure of the blastocyst to attach itself to the uterine mucosa. Stockard's view is that the lack of oxygen is the principal factor. Newman, while admitting that this may play a direct part, believes that the true cause is the "failure to attain at the proper time the essential growth stimulus which is normally supplied by placentation." The failure of placentation is in turn ascribed to some abnormality of the corpus luteum, a suggestion that had already been made by Stockard. As Newman points out, we must next look for a

cause for the behavior of the corpus, and so on ad infinitum. The endless chain, however, is all the while getting further and further away from any relation to polyembryony, and it is profitless to attempt to pursue it in this connection.

Much of the difficulty in analyzing the value of this theory lies in the indefiniteness of the language used. Newman accuses Stockard of using "intangible morphological conceptions," citing as examples such terms as "discontinuous mode of development" and "developmental arrests;" yet, in the succeeding pages he makes use of the even more nebulous phrases "partial loss of polarity" and "physiological isolation of growing regions." The criticized "discontinuous development" used by Stockard is replaced by Newman with "cessation of development." The average reader will find little choice between the two theories, for merely redescribing a morphological process of development in new and unfamiliar language adds nothing at all to our knowledge of the causes of the process. To say that there is a "physiological isolation" of growing regions is merely saying in a roundabout way that more than one embryo develops from a single primordium, and does not answer the question as to why there are more than one.

Either despite or because of the intangibleness of the concepts expressed in the theory, this hypothesis of Newman's has gone practically unquestioned. This has been partly due to the lack of any wholly satisfactory explanation of twinning, partly no doubt to a mistaking of turbidity for profundity. So far as I have been able to find, the only denials of the validity of the theory have been made by Hamlett (1929), from a consideration of the badger, and by Fischer (1931), from a comparison with some European mammals. These criticisms will be considered in a later section.

EVIDENCE FROM THE ARMADILLO

That the deficiencies of the uterine environment or the failure of implantation is the cause, directly or indirectly, of the stoppage of development of the ovum is implied or stated at various places in the papers of Stockard and Newman. This, however, is not true, as mitotic activity ceases some time before implantation would normally occur. Most of the blastocysts studied have come from the uterus, but Patterson and the writer have each obtained a few blastocysts which were washed from the tube. These vesicles average as large, and the cells of their inner cell masses are as numerous, as the average of uterine blastocysts. In other words, the development of the ovum comes to a standstill before it leaves the tube, at a time when the impending failure of implantation could affect the vesicles only if we credit the latter with a teleological power of foresight. Certainly this cessation of development cannot be due to the physiological effect of a missing stimulus whose presence is not yet due.

Not only is the quiescent stage initiated at the wrong time for the Newman-Stockard theory, but the actual conditions under which the vesicle passes this period are different from those postulated by the above mentioned workers. Both Stockard and Newman, the former in particular, have made much of the fact that the vesicle lies "free" in the uterine cavity, and have taken for granted a resultant lack of respiratory or excretory exchange as being responsible for the arrest of development and the loss of dominance or deaxiation of the supposedly single original axis. The deficiencies of this environment in respect to the possibility of exchange of gases

and metabolic by-products have been exaggerated due to a misconception of the actual conditions within the uterus. In the pregnant organ, the bloodvessels which supply its walls are engorged with blood and the whole uterus is turgid and saturated with plasma. The walls are thicker than in the non-pregnant animal, so that although the uterus is considerably larger in cross section, its lumen remains a small slit-like pocket filled with plasma in which the vesicle is bathed. The blastocyst is thus in as favorable an environment for respiratory exchanges or nutritive and excretory activities as is the average body cell, which has likewise only an indirect connection, through the intercellular plasma, with the blood stream. Furthermore, the blastocyst is not completely out of touch with the uterine mucosa. If a uterus containing a free vesicle be opened carefully the vesicle will be found actually in contact with the mucosa of the fundal area. There is, of course, no organic attachment; the blastocyst possessing merely enough adhesive power to retain its position. This adhesion is strong enough so that the vesicle sometimes does not come off in a salt solution until washed rather forcibly. The application of a fixing fluid, however, always suffices to separate the vesicle from the mucosa unless the trager cells have begun to function.

It is usually considered that a degree of relationship between trophoblast and mucosa as slight as described above is insufficient to allow the development of the embryo. It is true that in most placentates the ovum sooner or later develops a more intimate connection with the maternal bloodstream; but it must not be forgotten that in almost the entire group of the Marsupials we find conditions comparable to those described above for the armadillo. In the opossum the embryos are so loosely adherent to the uterus that if we make a short incision on either side the contraction of the uterine musculature is sufficient to expel every fetus in that horn. In spite of this seemingly inadequate provision for nutrition, the opossum embryo develops in a few days to a stage where it is able by its own exertions to travel from vulva to pouch, find a nipple, and attach itself. If the opossum ovum is able to proceed this far in its development, with no better system of obtaining food and oxygen than is found in the armadillo uterus early in pregnancy, then we cannot assume that it is the lack of these that causes the halt in its development. Some other factor must be sought.

In this connection, we should remember that even in the placentates there is at least one form, the pig, in which implantation never occurs. There is never any fusion between trophoblast and uterus, nor any erosion of the latter. Yet this lack of implantation does not retard development, nor does it induce polyembryony.

It may be pointed out here that out of the many hundreds of opossum eggs collected by Hartman, only one case of polyembryony was found—this in a form which should be extremely favorable for twinning if lack of implantation really plays any rôle as a causal factor, according to Stockard's interpretation of conditions in the armadillo.

Another point to be considered is the constancy of the process of polyembryony in the two species of Dasypus. In the nine-banded armadillo, the number of embryos is typically four. Variations from this number are very infrequent. In a series of 114 vesicles, old enough so that the number of embryos could be determined, one showed 5 embryos and one

showed 3. In a few vesicles in advanced development there may appear to be fewer than four embryos; these are usually cases of death in utero of some of the embryos. I have seen only one case of a vesicle showing two or three embryos where it was not possible to find the macerated or partially resorbed remains of the remainder of the set. The production of four embryos seems to be practically constant for this species. In a very few cases three or five embryos may be formed; there is no case known where less than three, or more than five, primordia were laid down.

The production of four (or rarely five) embryos is not the only constant feature about the embryology of *D. novemcinctus*; in this species the manner of origin of the primordia seems to be invariable. We may condense the following account from Patterson's description of the process. Soon after the hollowing out of the amniotic vesicle, we find this becoming elliptical and the floor of the cavity thickening at the two ends and thinning out in the center. These two thickened regions are the primary buds. Following this phase, a further shifting of cells of the primary buds gives rise to two secondary buds from each of the primary ones; these secondary buds, incidentally, have a definite position with respect to the original bilateral symmetry of the amniotic vesicle that was established with the appearance of the primary buds. The thickened ectoderm of the four secondary buds becomes the four embryonic shields of the four embryos.

In this species, the regular sequence of events in the process of budding off the embryonic primordia, the fixed orientation of these primordia to each other and to the original symmetry of the vesicle, and the almost invariable number of the embryos produced, are points which suggest that the mechanism of this development is under the control of some factor which is not easily swung aside from its predetermined course. Can this factor be a variation in the amount of oxygen available, or in the concentration of excretory products—factors which must vary widely according to the physiological condition of the maternal organism? Or can it even be the more uniform stoppage of development? A comparison with the conditions found in the other species of Dasypus will help us here.

In the South American mulita, *Dasypus hybridus*, Fernandez has shown that there are from seven to twelve embryos formed. As has been pointed out by Fernandez, and Newman calls attention to this in the earlier *Biology of Twins*, the embryos show absolutely no regularity in the manner in which they bud out from the ectodermic vesicle. Fernandez says on this point, "die Ectodermanlagen der Embryonen der Mulita ganz unregelmässig aus der primären Ectodermblase hervorwachsen, ohne jene bilaterale Symmetrie." Fernandez gives photographs of reconstructed models showing this point beautifully. His monograph is, unfortunately, not in wide circulation; but the interested reader can usually obtain the *Biology of Twins* which gives, on pages 74 and 75, outline drawings copied from Fernandez and showing the essential points mentioned above.

It is unfortunate that we know so little of the early part of the reproductive cycle in this species. Fernandez has never described a free vesicle stage in the mulita, and we have only his description of some ovaries of this animal on which to base our conclusions. In his first article on the embryology of the Edentates Fernandez calls attention to the fact that there is only one corpus luteum present. He then goes on to make the observation that the corpus must persist for a long time after

parturition, for it is found in animals killed a month and a half or two months before the beginning of pregnancy! In the light of what we now know about the early history of the ovum in the Texas armadillo, Fernandez' observation can only be interpreted as meaning that ovulation takes place some time before implantation, and that the mulita has a quiescent stage comparable to that in our species. If our inference is correct, we have two species with the same peculiar interruption of development, yet one of these species produces a quite variable number of embryos in an extremely haphazard relation to the common vesicle, while the other produces a much smaller, almost invariable number of embryos which always show a definite mode of origin from the ectodermic vesicle. Now no amount of "physiological isolation of growing regions" can explain why under the same conditions one species should have four embryos while the other has from seven to twelve. Neither can we understand why the manner of origin of these embryos should be so invariable in the one and so irregular in the other species if they are called directly into existence by the reaction of the blastocyst to a physiological condition which is apparently the same in both. Evidently these differences must be due to some intrinsic difference between the ova of the two species, or, in other words, to some hereditary difference between them; and this raises the suspicion that the whole process may be genetically controlled.

The fixity of polyembryony in these two armadillos is in marked contrast to the extreme uncertainty of its appearance under experimental conditions. I shall not attempt to analyze the work of Stockard on Fundulus or of Newman on Patiria, but shall merely point out that while these workers found it comparatively easy to cause abnormal development they were unable to induce the appearance of double monsters other than in an extremely haphazard and sporadic fashion.

In connection with the above mentioned regularity of the budding process as seen in the Texas armadillo, there is one feature which is in direct opposition to the hypothesis of arrested growth as the cause of multiple embryo formation. With the resumption of development following implantation the ovum proceeds to the formation of a single amniotic vesicle whose structure gives no hint of its impending budding. This lag in the appearance of the embryonic anlage is not unprecedented, however, as this delayed effect has been described by Stockard in his experimental production of double monsters in Fundulus. The supposed effect of the quiescent period is seen in the differential thickening of the floor of the amniotic vesicle to form the two primary buds. Now according to the theory, this rearrangement of the structure of the vesicle to form two new growing points should be followed by the development of these points into two embryos, for the rearrangement of cells and the establishment of the new axes of symmetry is supposed to cause the ovum to return to a condition in which it is ready for development. Instead of this we find these two active embryonic regions each bifurcating without any antecedent pause in their growth. Even if the formation of the primary buds were induced by the pause in development during the free vesicle stage, this pause could not explain the origin of the secondary buds; for their appearance is preceded by the resumption of cellular activity and the complete rearrangement of the embryonic structures, and this must preclude any effect of the quiescent period being transmitted beyond the time of the first rearrangement

of the blastocyst's symmetry. If all four primordia appeared simultaneously as primary buds from the vesicle we should not be able to rule out their possible causation by the stoppage of growth; but a consideration of the actual time of their appearance eliminates the possibility of the Newman-Stockard theory applying to the origin of the definitive primordia.

DELAYED IMPLANTATION AND POLYEMBRYONY IN OTHER MAMMALS

Despite the evidence presented in the foregoing pages, the strongest proof against the physiological theory of twinning comes from a comparison of the armadillo with certain other species. We already know of three placentates which resemble the armadillo in the presence of a quiescent period in their development, but which are not polyembryonic. In addition to these three forms, there is strong evidence for a similar history in eight species of martens and bears. This evidence may be found in papers of Ashbrook and Hanson and of Prell. We shall consider here only the species for which the embryology has been definitely worked out.

In 1854, Bischoff, in searching for the early stages of development of the European roe-deer, made the interesting discovery that the egg underwent an arrest of development during which it lay free in the uterine cavity. The arrest lasts from early fall until December, Bischoff describing it as occurring when the egg had reached the morula stage. As in all the deer, twinning occurs in the roe-deer, but is by no means the universal rule, and such twins are dizygotic. Bischoff's findings have since been confirmed by Keibel and others. This rather inconvenient exception to the theory of delayed implantation is explained by Stockard as not exhibiting polyembryony either because the stage when the delay takes place is not certain, although Keibel is quite definite on this point, or because of a "lack of tendency to form accessory embryo buds" (heredity). I have been unable to find a reference to Bischoff or Keibel in either of Newman's books.

The next reference to a delayed period in the development of the fertilized egg is found in a little known article by Fries, published in 1880. I have seen no reference to this work by either Stockard or Newman, and the results seem to be unfamiliar to most workers in this country. Fries was interested in the delayed fertilization described by several European investigators in the bats. He apparently reached the conclusion that the delay was in some way an adaptation to the hibernating habit, and in pursuing this line of thought he made a study of the European badger, *Meles taxus*, an animal which hibernates. The badger, however, proved to be unlike the bat and similar to the roe deer. Fischer has followed up Fries' discovery, and has recently published a complete account of the reproduction cycle. I give in the following paragraph a summary of Fischer's findings.

Meles breeds during the months of July and August; individuals killed at the end of that month or at the beginning of August have usually ovulated. Ova examined between then and December have not implanted, but lie free in the uterus, in a stage corresponding to the inner cell mass blastocyst of the armadillo. No embryos are to be found before December, implantation taking place during that month. The young are born about March 1. The number of corpora lutea and of ova was always larger than the usual number of young for the species, also the older vesicles observed have all been monoembryonic.

Fischer discusses the bearing of these findings upon Newman's theory as to the cause of twinning. He points out that both the badger and the roe deer exhibit a long delay in development, and yet polyembryony is not known to occur in either of these forms. Fischer concludes that Newman's hypothesis is untenable, and that twinning in the armadillo is the result of factors intrinsic in the egg.

The third species known to exhibit a free vesicle stage is the American badger, *Taxidea taxus*. The earliest part of the cycle is unfortunately still unknown, but it has been shown (Hamlett, '32) that unimplanted blastocysts are to be found throughout December and January, implantation taking place about the middle of February. A study of embryos from the primitive streak until just before birth shows the vesicles uniformly producing each a single embryo. Like Fischer, the author has pointed out (Hamlett, '29, '32) the significance of this reproductive cycle to the theory of twinning advanced by Stockard and Newman.

In the three cases cited above we have animals with delayed development which are not polyembryonic. Let us consider briefly the reverse of these cases. Besides the armadillos there is only one form known in which polyembryony occurs as a regularly occurring phenomenon; this is in the case of certain human stocks. It is known that in some families the production of single ovum twins follows the laws of heredity. It is unnecessary to review the evidence for this; those interested will find it presented and the literature reviewed in papers of Davenport and of Dahlberg. It has been shown that twinning, as well as the higher forms of polyembryony, is transmitted through either parent and that it will reappear in certain lines for generation after generation. In the light of all the evidence that has been accumulated, Newman's statement that the genetic theory of human twinning seems "fantastic" cannot be taken seriously.

Because of the situation presented by the armadillos, the question immediately arises as to the possible occurrence of delayed implantation or retarded development in cases of human twinning. Newman assumes that this retardation actually occurs. While our actual knowledge concerning the early embryology of human twins is, unfortunately, almost nil, we do possess certain statistical evidence that has a bearing on the topic under discussion. Not only is there no evidence that the length of gestation of twins is longer than the norm, but as a matter of fact, twins are very often born several days or weeks before the end of the usual two hundred eighty days. Some obstetricians place the percentage of these premature births as high as seventy-five or eighty per cent of all plural pregnancies. Under such conditions any period of delayed development at all comparable in length to those found in the armadillo or the other species named above would be incompatible with the production of viable children.

In view of the foregoing facts it is evident that we must recognize the association in the armadillo of discontinuous development and polyembryony as being purely fortuitous. The cases of the roe deer and the badgers show that polyembryony does not always accompany quiescence of the blastocyst, and a consideration of human twins renders it extremely unlikely that quiescence accompanies polyembryony in this species. Even in the armadillos there is seen to be a variation between species in the method and extent of polyembryony, while each species is relatively constant under varying conditions. In man we find that the occurrence

of one egg twinning is inherited, and that the factor may come from either parent. The exact number, and perhaps the mode of origin of the embryos varies from one species to another. Thus we find the Texas armadillo producing four young by a definitely oriented process of budding; the mulita producing a higher, variable number through irregular budding; and some lines of the human species producing twins, whether by budding or by some other process we are at present unable to say. The essential feature is that for each form it is a definitely determined process, not dependent upon hit or miss variations in the environment.

DISCUSSION

The preceding pages have shown the inapplicability of the Newman-Stockard theory to the case of the armadillo, and the lack of agreement between the armadillo and the other mammals which show delayed implantation. It now becomes our problem to devise some explanation that will fit the facts already brought out and at the same time be as simple and logical as possible. In evolving this explanation there are three sets of comparisons that are of particular significance: the comparisons of the mulita with the nine-banded armadillo, of the two armadillos with twinning families in the human, and of the armadillos with such mammals as the roe deer and the badger.

In the first case, that of the mulita and the nine-banded armadillo, we find two closely related forms, each with a delay in its embryology and each reproducing by polyembryony; but the number of young and the relations of the embryonic diverticula differ in the two species, also the process is quite regular in novemcinctus and irregular in hybridus. That is to say, in these two forms the blastocysts develop under apparently identical conditions, yet they show differences which are as specific as any purely morphological features characteristic of the adults. Since these differences appear under identical physiological conditions and with the same interruption of development, it is evident that the different types of polyembryony found in these two species must be due, not to the physiological conditions under which the blastocysts develop, but rather to some inherent difference between the ova of the two species.

When we compare the species of Dasypus with human identical twins we see the case from another angle. Here we find both types developing polyembryonically, but one form has a long period of delay while the ova of the other show a continuous development. Here too we must invoke some inborn factor that will carry these eggs to a similar goal under widely different physiological conditions.

The reverse of this, finally, is seen when we compare our two armadillos with the roe deer or the badgers. Here we find a group of animals, all of which show an interruption in development, yet only the armadillos are polyembryonic. Once again we are forced to conclude that there must exist within the armadillo ovum some quality that causes it to give rise to quadruplets (or more, in hybridus), while those of other species under apparently identical conditions, show no slightest tendency toward twinning.

The foregoing three lines of evidence all unite in indicating that in Dasypus, and in certain human families, the ova possess some fundamental twist in their organization that causes them to develop polyembryonically irrespective of their physiological environment. Since this peculiarity of the ova reappears regularly in each generation, it fulfills the requisites of a hereditary character, and as such it is undoubtedly controlled by some gene or set

of genes. In the armadillos, where the two species under consideration seem to be homozygous for this character, verification of this by breeding experiments would seem to be impossible. In man, however, sufficient pedigrees have been collected, as noted previously, to confirm this conclusion. As is the case with the great majority of genes known, the reaction set up by this gene (or genes) is of sufficient intensity and stability so that it is not affected by environmental variations within the limits which allow development to take place at all.

The foregoing should not be interpreted to mean that all uniovular twinning is the result of definite hereditary forces. There are cases where an egg, designed by Nature to form a single embryo, has through some accident of cell division or of environment, through injury or death of cells, given rise to two or more embryos or parts of embryos. Such are the various types of double monsters and Siamese twins; doubtless some of these cases give rise to completely separated, normal embryos. Failure to recognize the accidental nature of these pathological cases has caused Newman to try to interpret the cause of the perfectly normal course of specific polyembryony in terms of the abnormal conditions which frequently accompany (and cause?) the production of double monsters.

Certain facts should be clearly understood at this point. Double monsters are unknown from the armadillo, although they should be very abundant if they are due to the same causes which produce the quadruplets. Double monsters are not found in human twinning families any more commonly than in the general population. Double monsters do not run in families as does twin production. The conclusion seems inevitable that the production of double monsters is not due to the same causes as is specific polyembryony. The first is accidental, specific polyembryony is the result of a definitely inherited genetic factor.

A word of explanation would seem due at this place in regard to the use of the term "physiological" in the title. The use of this word in distinction to "genetic" is not intended to imply that twinning is not associated with a profound modification of the usual physiology of development. Newman has unfortunately used the term (e.g., "Physiology of Twinning") as if it meant that the mechanism of development is so little fixed in the organism that it can be swung from monoembryony to polyembryony by mere changes in oxygen concentration or speed of development. It is the conclusion of the writer that polyembryony is dependent upon some genetic factor or factors, and is inherited as definitely as is, for instance, eye color. Just as eye color is dependent upon the physiology of the pigment-forming cells of the iris, so the series of cell divisions and cytotaxic shiftings that result in the formation of four embryonic primordia instead of one may be said to be an expression of the physiology of the developing blastocyst. But to pursue our reasoning a step further, just as the physiology of the iridial cells is directed by a definite gene (or set of genes) that determines that the cells shall or shall not lay down brown pigment, so the complex of physiological activities that we speak of as embryonic development is governed by definite genes that rule these activities as determinately and irreversibly as eye color in man or in fly is painted by its appropriate genes. We realize that eye color is due to the physiological behavior of the pigment cells producing certain morphological results; but we also know that this activity is determined by definitely inherited particles of chromatin; consequently, we think of eye color as

being the product of a genetic process. The same must be true of polyembryony. Newman's view is apparently that the genetic factors are negligible in determining the number of embryonic primordia produced; he says in one place that the idea of the inheritance of twinning is "fantastic." On the other hand, Newman is willing to believe that lack of oxygen, excess of carbon dioxide, the accumulation of wastes, or a variation in the rate of development is sufficient to so completely transform the course of development as to bring about polyembryonic growth. I feel convinced that the processes of embryo formation are so firmly ingrained in the organism that they are not capable of being affected by any variation in environment unless that variation is so profound as to completely upset the mechanism of development. The factors which Newman terms "physiological" may by their aberrations produce monstrosities; they can not bring about the regular and exact formation of several perfect embryos from the single egg as we see done in the armadillo. The physiology of twinning is not dependent upon external factors of the environment, it is governed by the intrinsic hereditary potentialities of the fertilized ovum.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that* THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

THE FELIDÆ OF RANCHO LA BREA. *Carnegie Institution of Washington Publication No. 422.*
By John C. Merriam and Chester Stock. Carnegie Institution of Washington, D. C. \$7.00 (paper); \$8.00 (cloth). 9 x 11¾; xvi + 231 + 42 plates; 1932.

In the Introduction to this fine addition to the Carnegie publications the authors say:

> Were one to select any single item to illustrate the most striking phase in the long list of exceptional features of our North American Pleistocene life as exhibited by the Rancho La Brea fauna, it would presumably be the representation of the Felidae. Excepting only the dire wolves, no group in the fauna of Rancho La Brea is represented by such a multitude of specimens, ranging up to more than one thousand individuals of the sabre-tooth cat and an exceptionally large number of individuals of the great lion-like cat, with a limited number of smaller types.

From this abundance of material, almost perfectly preserved in the asphalt deposits of Rancho La Brea, measurements of every skeletal part of representative individuals were made and are recorded in detail, both numerically in the text tabulations and pictorially in the excellent photographic and heliotype plates. Minute quantitative and qualitative comparisons are made both between specimens found in the Rancho La Brea and other North American deposits. For the comparisons, the various skeletal parts are considered collectively in separate sections of the book, but adequate cross reference numbers permit the study of all available measurements of a single individual animal. The book is thoroughly documented; it is beautifully printed; and the pen and ink and wash drawings by John L. Ridgway and the restoration drawings by Charles R. Knight are exceptionally well done.

DARWINS THEORIE DER GESCHLECHTLICHEN ZUCHTWAHL IM LICHTE DER HEUTIGEN FORSCHUNG. *Zugleich eine Untersuchung über das "Manometerprinzip" der Sexualselektion.*
By N. G. Lebedinsky. Martinus Nijhoff, The Hague. 13.60 guilder. 6⅝ x 9½; 244; 1932 (paper).

A review of the more important recent studies on the mechanisms operating in sexual selection. The following are among the more important conclusions.

> The secondary sexual characters attain their most luxuriant development, and the gonads and their products the greatest functional and healthy level, only with entirely normal metabolic constitution of the organism. This sensitivity of characters of an esthetic nature determines their inner selectional worth. Even though the females certainly choose their mates subconsciously, the fact that their taste is based on a "health and strength meter" facilitates a selection advantageous to race hygiene. Unconsciously the females choose healthy fathers for their offspring and thereby assure the success of species stability. [This is the essence of the "manometer principle."]
>
> The causes of the primary genotypic origin of esthetic sexual characters are, like those of mutation generally, unknown. Their appearance (whether it concerns entirely new characteristics or a functional change of already existing marks of differentiation of species and sex) in only one sex appears to be bound, at least in part, to differences in the general metabolism of the sexes.

This is an important book. It is equipped with a bibliography covering twenty pages, author and subject indices.

THE CEPHALASPIDS OF GREAT BRITAIN.
By Erik A. Stensiö. British Museum (Natural History), London. Three pounds. $9\frac{1}{2} \times 12\frac{1}{8}$; xiv + 220 + 66 plates; 1932.

This monograph based on material belonging to museums and private collections is of great interest and importance because of the antiquity and primitive characteristics of the cephalaspids, and their bearing on the evolution of vertebrates. A great many of the specimens are beautifully preserved with the result that it has been possible to work out the morphology with amazing detail and thoroughness. The work is liberally illustrated. The plates are superb. The first part of the memoir is devoted to a detailed discussion of the anatomy, and the second part to the taxonomy of the group. There is a final section comparing the cephalaspids with other ostracoderms. Altogether this is a contribution of the first rank to the literature of paleontology.

ASPECTS OF EVOLUTION.
By F. W. H. Migeod. Heath Cranton, London. 5s. net. $4\frac{7}{8} \times 7\frac{1}{2}$; 127; 1932.

The point of view and thesis of this book are contained in the following quotation from the final chapter:

> Evolution as a special theory has sunk from its position of being a mechanistic process of itself to being merely a paper record of accomplished facts. Creativeness is an all-pervasive force in nature, and creation is its outcome. In consequence, therefore, it would be difficult to recognize the creation of matter, life and mind without accepting a maker thereof, who may work by any of the various methods we find have been employed.

According to the author, mind is the chief factor through which change takes place. Habit, mimicry and homoplasy also assist. The author's sources appear to be almost entirely derivative, text-books and general treatises rather than original sources, but biologists may find a good deal of interest in reading a statement of the creationist argument, consistently and temperately developed. The author is an anthropologist.

DER WEG DES MENSCHEN VOM LINKS- ZUM RECHTSHÄNDER. *Ein Beitrag zur Vor- und Kulturgeschichte des Menschen.*
By Richard Kobler. Moritz Perles, Vienna. 7.50 marks (paper); 9.50 marks (cloth). $6\frac{1}{4} \times 9\frac{1}{2}$; ix + 142; 1932.

An attempt to prove that the prehistoric members of the human species were left-handed, and to trace the evolution of the transfer of [assumed] left-handedness to right-handedness. The author attacks the problem from several viewpoints, as indicated in the following chapter headings: The superiority of one hand—a characteristic of man; Prehistoric man—a left-handed person (based on a study of implements of the Stone Age); Right-handedness—a consequence of the use of weapons; The physiological foundations of right-handedness—critically viewed; Present-day left-handedness—a relic fauna; Left-handedness in the mirror of the cults; Cultural-philosopical views. The book is furnished with an eight-page bibliography, and author and subject indices.

GENETICS

THEORETISCHE BIOLOGIE. *Erster Band: Allgemeine Theorie, Physikochemie, Aufbau und Entwicklung des Organismus.*
By Ludwig v. Bertalanffy. Gebrüder Borntraeger, Berlin. 18 marks (paper); 20 marks (cloth). $6\frac{1}{2} \times 10$; xii + 349; 1932.

A well-written and stimulating discussion of the present state of the fundamental concepts and problems of general biology. The author aims to summarize the existing theories in the various fields in the hope that this may aid toward the formation of an adequate general theory of life. The mechanistic, vitalistic, and *Gestalt* theories, taken separately, he shows to be inadequate. In this volume, after a critical

discussion of these theories, he proceeds to consider the physical chemistry, organization and embryonic development of living organisms. The author's philosophy leans, as is well known, towards the "organismal" position, and the temperate and scholarly development of the argument seems singularly sound and refreshing in a world bombarded with genes. This volume has its own bibliography.

GENERAL BIOLOGY

GROWTH.

By James L. Smith. Edited by J. S. Haldane. Oliver and Boyd, Edinburgh. 6 shillings net. $5\frac{1}{2} \times 8\frac{3}{4}$; vii + 135; 1932.

Professor Smith, during the last years of his life, was engaged in the preparation of a book on growth, which, unfortunately, was left unfinished at the time of his death. The manuscript of the introduction and fourteen chapters, although unrevised, were in completed form, and together with a final summary chapter by the editor, are presented in this book. In discussing the author's purposes, Professor Haldane remarks, "Seeing clearly that the key to the problem of normal growth is the understanding of life itself, he had meant the book to embody the general conclusions which he had formed as to the nature of life, and the bearing of these conclusions on the abnormal forms of growth with which pathology deals." In another place the editor says, "I can confidently say that it was Lorrain Smith's ideal to make the distinctive conception of life the basis of pathology, just as it has been my own ideal to make this conception the basis of physiology." Taken at face value the book scarcely can be said to attain its ideal, or even to make a clearcut consistent approach to it. It is, for example, far from clear whether growth is to be interpreted as meaning cell division, simple increase in cell size, or increase in the size of an organism by both enlargement and multiplication of cells. In the discussion of variation, height is considered to "approximate so closely to the average that stature is one of the most definite elements of human heredity." Certainly it may be questioned whether or not any scale of variation has been devised by means of which it may be shown definitely that one organic element is more or less variable than another. In the final chapter of the book, the theory is advanced, with scant reference to previous work, that malignant tumor cells arise as the result of injury to chromosomes which is transmitted from cell to cell as a mutation. There is a short list of references but no index. It is to be regretted that the opportunity was not taken to add to the book a bibliography of Professor Smith's publications.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 401. Methoden der Süsswasserbiologie.* Containing following articles: *Das limnologische Laboratorium in Aneboda*, by Einar Naumann; *Die Untersuchung des Stoffwechsels der Wasserbakterien*, by Adolf Seiser; *Die Exkursionsuntersuchungen des Limnoplanktons*, by W. M. Rylov.

Urban und Schwarzenberg, Berlin. 8.50 marks. 7 x 10; 156; 1933 (paper).

Naumann's description of the limnological station at Aneboda, in southern Sweden, is meant to serve as a guide in planning small biological stations for the study of fresh water biology. There are numerous photographs and several ground plans of buildings.

Seiser discusses the cultural methods applicable to the water bacteria whose metabolism is so bizarre that they can live on hydrogen, carbon monoxide, paraffin, or phenol, as well as methods for the more prosaic forms that merely live on nitrogen, iron, sulphur or cellulose.

Rylov, of Leningrad, contributes a delightful article on what the well equipped biologist will carry when he goes on field trips to study fresh water biology. How many know that a folding chair, which can be carried in the indispensable *Rucksack*, is desirable? If you can get another person to carry it, you can take a collapsible boat with you, Rylov explains. We can heartily recommend this chapter to all unimaginative biologists who have never been on field trips but who think it might be nice to go sometime.

Physical Chemistry of Living Tissues and Life Processes. *As Studied by Artificial Imitation of Their Single Phases.*
By R. Beutner. The Williams and Wilkins Co., Baltimore. $5.00. 6 x 9; x + 337; 1933.
Professor Beutner has revived an old dogma, that the way to understand a process is to make a model of it. There is a bit of the revivalist in his manner, including a firm conviction in his message, and an enthusiasm that is forever breaking out into whole paragraphs of italics. The use of analogy used to be called the preacher's fallacy; it is Beutner's hope that the use of physical analogies may become a major part of physiological research. He has made a collection of imitations of vital phenomena with the materials and equipment of chemical and physical laboratories. It falls under three main headings: models based on membranes, osmosis, and related forces; life processes related to crystallization or due to surface forces (here are placed respiration models and imitations of amoeboid movement); and a third section devoted to bioelectric phenomena. It is instructive to read through the indexes, the author index in particular, to see who is left out. Herrera gets a bare mention, MacDougal is left out, and the successful models of the ascent of sap are not in, either, although Gurwitsch and his mitogenetic rays receive a whole chapter, curiously enough.

The Action of the Living Cell. *Experimental Researches in Biology.*
By Fenton B. Turck. The Macmillan Co., New York. $3.50. $5\frac{3}{4}$ x $8\frac{1}{2}$; xi + 308; 1933.
We devoted a good deal of space to the discussion of the late Doctor Turck's opinions in an earlier issue (Volume I, pp. 603–608) and this book does not show any essential change in point of view in the intervening time. It does, however, show two things: (1) If you believe in a theory strongly enough you can bring anything in human experience into accord with it; (2) Doctor Turck seems never really to have apprehended what a control experiment meant.

The Mechanistic Autonomy of Nature.
By Carl F. Krafft. Carl F. Krafft, 2510 Q St., N.W., Washington. $1.00. $5\frac{3}{8}$ x 8; 101; 1933.
This book presents a discussion of the essential nature of living matter and life processes in which the Deity as a basic factor is definitely eliminated in favor of the "unalterable principles of geometry and statistical mechanics." On the whole it would appear that, as between Mr. Krafft's "spirazines" and Jahweh in the exegesis of knotty biological problems, honors are about even.

A First Book of Biology.
By Mary E. Phillips and Lucy E. Cox. University of London Press, London. 2s. 6d. net. $4\frac{3}{4}$ x $7\frac{1}{4}$; 270; 1933.
A simple introduction to biology for the young. The authors believe that the best approach is through nature study. Consequently no plant or animal is described that cannot be easily seen. The material is treated from a seasonal standpoint. As a further stimulation for children there are scattered through the book simple and easily executed experiments.

Données Numériques de Biologie. Biology, *extracted from Vol. VIII (1927-1928) and IX (1929) of the* Annual Tables of Constants.
By E. -F. Terroine and M. -M. Janot. Gauthier-Villars et Cie., Paris. 90 francs. $8\frac{3}{4}$ x $10\frac{1}{2}$; xxi + 129; 1932.
Volumes V, VI and VII have already been reviewed in Volumes II, IV and VI respectively of this Review. Volumes VIII and IX deal with those biological constants reported for the years 1927 to 1929. A wide variety of phenomena are treated, as in previous volumes. The compiling and editing have been carefully done. The series is a useful one.

Mers et Océans.
By Camille Vallaux. Les Éditions Rieder, Paris. 20 francs (paper); 25 francs (cloth). $6\frac{1}{8}$ x 8; 100 + 60 plates; 1932.

An excellent brief account of the seas, their dominion and depth, movement and content, their effects on climate and on the lives of people involved in marine industries. The book is profusely illustrated with photographs of real aesthetic value. There is a bibliography of 25 titles.

HUMAN BIOLOGY

LES FRAUDES EN ARCHÉOLOGIE PRÉHISTORIQUE *avec Quelques Exemples de Comparaison en Archéologie Générale et Sciences Naturelles.*

By A. Vayson de Pradenne. Émile Nourry, Paris. 75 francs. $6\frac{1}{2} \times 10$; 676 + 46 plates; 1932 (paper).

The greater part of this book consists of detailed and well documented narratives of frauds in prehistoric and general archeology. For comparison in the field of the natural sciences the celebrated case of Kammerer and *Alytes obstetricans* is presented. Having gathered his facts the author analyses them. The swindler and his motives, the dupe and the means by which he is ensnared, the unconscious leads which he gives the swindler for the development of the fraud, the specious arguments by which he supports the authenticity of the discoveries when they are called into question, are all analyzed with great skill and shrewdness. The final section is devoted to the technique of detecting fraud in archeology.

The book will be of undoubted value, not only to the archeologist, but to all who have the task of sifting truth from error. Much of it is, moreover, amusing reading, as, for example, the account of the 27,000 forged letters of such personages as Pontius Pilate, Mary Magdalen, Sappho, and Cleopatra which were bought for 140,000 francs by the celebrated French mathematician, Chasles. But perhaps the most amusing tale is that of the discovery in the valley of the Clyde of inscribed shells and other supposed prehistoric remains. The controversy over their authenticity raged for several years—Andrew Lang being one of their most impassioned defenders—until Boyd Dawkins discovered that the supposed prehistoric shells were those of Blue Point oysters and pointed out that either the importation of American oysters to Scotland began before the discovery of America or the finds were forgeries.

FLESH OF THE WILD OX. *A Riffian Chronicle of High Valleys and Long Rifles.*

By Carleton S. Coon. William Morrow and Co., New York. \$2.75. $5\frac{3}{8} \times 8$; xi + 339; 1932.

This book tells a remarkable story, not alone entertaining to the reader, which would be a sufficient excuse for its writing, but full of interesting material for the thoughtful human biologist. For a young Ph.D. fresh from the university to trot serenely off to the upper bowels of the Moroccan Rif accompanied by a newly acquired and beautiful wife, live there all told more than a year, and come back still accompanied by the same wife, is to strain the credulity of those who do not believe in miracles. For the Riffians are tough babies, full of prejudices about strangers, particularly white ones, and nervous—not to say flighty—with the trigger finger.

However these amazing Coons got away with it. The technique of this book is to embody a great deal of sound Riffian ethnology, folklore and folkways into a connected account of the history of an imaginary family of the Vale of Iherrushen—a sort of Berber Forsyte Saga. And what a tale it is! The Riffian is a direct actionist. If he wants anything he goes and gets it; if someone annoys him it is just too bad for the widow and children. Inhibitions play but a small part in Berber behavior. And yet the account of the killing of a sister by her two brothers, because she had flaunted the code and slipped into ultimate amatory dalliance, shows how dreadfully rigorous the maintenance of standards of conduct may be among a people both unmoral and in many ways actively immoral.

We strongly recommend the book to our readers. It is cleverly and artistically illustrated with black and white drawings.

La Critica Medica nella Storia, Alessandro Magno.

By Mario Bertolotti. Fratelli Bocca, Torino. Lire 56. $6\frac{1}{4} \times 9\frac{5}{8}$; 413; no date (paper).

The author has studied the biographies of Alexander the Great; the records of his physicians; and those of Eumenes of Cardia, his secretary and general, who, it appears, kept a more complete record of the Emperor's illnesses and wounds than his physicians did. This book is a notable and interesting reconstruction of his biologic, psychologic and medical history. The author deduces from descriptions and statuary that Alexander was a hyperthyroid type, and may have been afflicted with wryneck. He can find no evidence for the belief that he was homosexual. During his campaigns Alexander received nine wounds, the most serious of which—a fracture at the base of the skull and a chest wound involving the pleura but not the lungs—are described in detail. From records concerning the latter, the author deduces that he also suffered from empyema. In connection with the former, the author raises the question of Alexander's intemperance. He advances the theory that he gained this reputation in the period following the skull fracture by falling asleep at the many banquets he attended. This habit is assumed to have been due to hypersomnia as a sequel to the injury rather than to excess consumption of alcohol. Just conceivably, as a further possibility, banquets may have been as dull then as now. Alexander's irritability and suspicion of friends in his later years are ascribed to the influence of his intimacy with a group of soothsayers rather than to physical ills. Alexander had malaria twice. The first attack is compared with that of Byron. The description, as reconstructed from records, of the attack of the tertian type which caused his death, is splendid. The book is illustrated with many excellent photographs of statues, busts, and masks. A bibliography and a glossary of clinical terms are appended.

The Personality of Britain: *Its Influence on Inhabitant and Invader in Prehistoric and Early Historic Times.*

By Cyril Fox. National Museum of Wales, Cardiff. 2s. 6d. $8\frac{1}{4} \times 10\frac{1}{2}$; 84 + 3 folding maps; 1932 (paper).

The prehistoric inhabitants of the British Isles and those who followed them left, quite unconsciously, remarkable gifts to the British anthropologist of today. So abundant and widespread have been the findings of the megalithic, bronze and early iron ages that it is now possible to predict with considerable accuracy where the early British types actually lived and labored and what determined their activities. In order to reconstruct the ancient picture comprehensively, however, it is necessary to take into consideration the profound differences in geography, climate, fauna and flora of megalithic times from the present day conditions.

In *The Personality of Britain* is given a general survey of all that investigation has revealed up to the present time concerning the different streams of culture which flowed into the eastern and western parts of the Isles and the effect which these cultures had upon those already established. In the highlands there tended to be a fusion of the invaders with those already established. In the lowlands the old culture tended to be replaced by that of the newcomers. The aloofness of Ulster from the general life of Ireland of today may have, according to the author, its basis in prehistoric times. Included in the work are many maps showing the distribution of the different types of early remains. The final map, in which there is an overprint of the distribution of antiquities of the Bronze Age, suggests that the British Isles may have been far more densely populated in that era than is generally assumed.

Indian Removal. *The Emigration of the Five Civilized Tribes of Indians.*

By Grant Foreman. University of Oklahoma Press, Norman. \$4.00. 6 x 9; 415; 1932.

This is not a pleasant chapter in the development of our country. Five Indian tribes from the states of Tennessee, Georgia, Alabama, Mississippi and Florida, representing about 60,000 individuals, were forced to leave their lands to which they

were deeply attached and journey west, across the Mississippi, up the Arkansas River, into what is now Oklahoma. Their removal commenced in 1831. About ten years later the last group had been transferred. Intense suffering and hardship were endured by peoples who had not only long ceased to be nomadic, but had achieved a high degree of cultural development. Mr. Foreman has gone to the original documents, reports and letters, for his material. Not all of those who forced these tribes out of their homes or assisted in their emigration were blackguards. Particularly the officers and soldiers of the Army showed sympathy and consideration for their welfare. At every turn, however, there were those who were ready to take advantage of their helpless condition, either by bribery, corruption of their leaders with whiskey, or by downright fraud. The account is largely an exhibition of white ignorance, tyranny and cruelty. Illustrations and maps add to the interest of the book. It is carefully documented and indexed.

Crimes and Criminals.
By William A. White. Farrar and Rinehart, New York. \$2.50 net. $5\frac{1}{2} \times 8\frac{1}{8}$; viii + 276; 1933.

The author has had wide experience in the practice of psychiatry and in dealing with mental patients from Federal prisons and military establishments. For nearly 30 years he has been in charge of St. Elizabeths Hospital, the government hospital for the insane, in Washington, D. C. A clear discussion is given of the fundamental principles "which must be taken into consideration in order that we may be able to think and act intelligently with regard to problems of criminology, be they the problems presented by crime in the abstract or by the criminal himself in the flesh." Dr. White holds that methods of punishment at present are largely a way of expressing what is at bottom vengeance and retaliation. Neither a prison, as it is now used, nor capital punishment are of any real value in crime prevention. All constructive work in the future must take into consideration the principle that destructive or dysgenic forces at work are offset by constructive or eugenic forces of equal strength. This principle, according to the author, has not generally been appreciated because the destructive force is so much more apt to be prominently in evidence. The first part of the book is valuable in clarifying the problem of dealing with anti-social people, and in showing what should not be done with our criminals. The latter part, dealing with penological principles and the trend of methods of crime prevention, is less satisfactory. Here we find much that is controversial. The book is briefly indexed.

History, Psychology, and Culture.
By Alexander Goldenweiser. Alfred A. Knopf, New York. \$5.00 net. $6\frac{1}{4} \times 9\frac{3}{8}$; xxiv + 475; 1933.

This book represents many years of deliberation by the author on social theory. Most of the essays have appeared previously. All of these have been completely revised. The volume is arranged in six parts, as follows: Part One, *History, psychology, and culture.* A set of categories for an introduction to social science; The principle of limited possibilities in the development of culture; Psychology and culture; Anthropology and psychology; J. Teggart's approach to history; Culture and environment. Part Two, *Theories of primitive mind and culture:* Cultural anthropology, Sir James Frazer's theories; L. Lévy-Bruhl's theories; Wilhelm Wundt's theories; Sigmund Freud's theories. Part Three, *Totemism:* Totemism, an analytical study; The origin of totemism; Form and content in totemism; A final note on totemism. Part Four, *Religion:* Religion and society: A critique of Émile Durkheim's theory of the origin and nature of religion; Spirit, "Mana," and the religious thrill. Part Five, *Race:* Race and culture in the modern world; Are the races potentially equal? Part Six, *Variora:* Man and woman as creators; Is Freud a psychologist? Civilization as some school-children see it; The new education.

The book concludes with an extensive bibliography, an index of names and one of subjects.

THE PROBLEM OF LEMURIA. *The Sunken Continent of the Pacific.*

By Lewis Spence. David McKay Co., Philadelphia. $3.50. 5⅝ x 8½; 249; 1933.

Mr. Spence writes of that area in the Pacific which at one time was occupied by a continent, or several great land masses. It included New Zealand at one end and Hawaii at the other. Far to the eastward Easter Island with its remarkable monuments gives indications that it was in the past closely linked with the now sunken region, and may have been the Mecca of an ancient race. The geological evidence that such lands once existed seems good. The book deals chiefly, however, with the evidence presented by a study of the archaic temples and statues which are still extant, and remnants of culture and legends preserved by native islanders. The present Polynesian race has many legends which indicate that these ancient people were of white stock. The colored folk were probably employed in great numbers in their vast building operations, since huge stones were often transported many miles in temple construction. The existing hieroglyphic writings have never been interpreted. Included in the book are some entertaining theories concerning Lemuria which various writers of the air-castle type have advanced. The volume is interestingly illustrated, and indexed.

HISTORY OF AGRICULTURE IN THE SOUTHERN UNITED STATES TO 1860. *Carnegie Institution of Washington Publication No. 430. Volumes I and II.*

By Lewis C. Gray and Esther K. Thompson. Carnegie Institution of Washington, D. C. $6.25 (paper); $7.25 (cloth), for set. 6⅝ x 10⅛; xxviii + 1086; 1933.

This history of agriculture is a record of the continuous process of experimentation that went on in the pre-experiment-station era. These experiments involved not only finding crops adapted to the soils and climate of a new region, but also a perennial search for profitable markets; and on the part of legislators they meant adjusting subsidies and taxes, and dealing with the recurrent problem of over-production. It will be a surprise to many to find out how many things people had to do for themselves without governmental aid. It will also surprise other people to learn just how long and how successfully governmental agencies have had to come to the support of agriculture.

Any brief estimate of so important a book is bound to be inadequate. It is so smoothly written that one almost overlooks the thorough documentation. It is written as a monograph on agricultural economics but Dr. Gray has interpreted his field broadly and it ought to be helpful to anyone interested in any of the numerous crops or kinds of livestock that were introduced into this region. There is a helpful index.

SOCIAL BELIEFS AND ATTITUDES OF AMERICAN SCHOOL BOARD MEMBERS.

By Claude E. Arnett. Emporia Gazette Press, Emporia, Kansas. $1.75. 6 x 9⅛; xvi + 235; 1932 (paper).

The social beliefs and attitudes, with regard to economic, international, educational, and other like issues at the forefront in American life today, of 1,076 American school board members were determined by the questionnaire-test method. The findings are reported in this publication in the form of descriptive and comparative analyses by means of the statistical method. Results are stated in terms of "conservatism" and "non-conservatism." There is a short bibliography.

A BIBLIOGRAPHY OF THE HONOURABLE ROBERT BOYLE, *Fellow of the Royal Society.*

By J. F. Fulton. Oxford (University Press). (Reprinted from the Oxford Bibliographical Society, Proceedings and Papers, Volume III, Part I, pp. 1-172). 7⅝ x 10; 172; 1932 (paper).

This detailed and beautifully printed bibliography is a fruit of the author's interest in Boyle's medical and physiological works. However, it is not confined to these but deals with all his writings, scientific and theological. The preliminary notes to each book give a brief

analysis of it and the author hopes that the bibliography "in describing Boyle's works systematically, may pave the way for some one who is willing to undertake the formidable task of assessing his scientific achievements." The volume is illustrated by reproductions of Rysbrack's bust of Boyle and of the title pages of many of his books. There is an index. The vital statistician will be interested to note that Derham's *Physico-Theology*, the connecting link between the work of Graunt and Süssmilch, was originally delivered as one of the courses of lecture sermons "to prove the truth of the Christian religion against infidels" which Boyle had endowed in his will.

Handschrift und Ehe. *Eine Lehre vom Zusammenpassen der Charaktere, dargestellt an Handschriften aus Gegenwart und Geschichte.*

By Bernhard Schultze-Naumburg. J. F. Lehmanns, Munich. 4 marks (paper); 5.50 marks (cloth). 6 x $8\frac{7}{8}$; 117; 1932.

According to the publisher's blurb many of the 30 to 40 thousand unhappy marriages ending in divorce annually in Germany could have been easily avoided if the handwriting of the partners had been analyzed before the wedding. The author of this book has devised a method of presenting in schematic form the analyses of character traits based on Klage's system of graphology. He illustrates the book with samples and analytical diagrams of the handwriting of the husband and wife in a number of historically happy unions, and several recent unhappy ones, and compares the traits, as shown in the diagrams, for compatibility. By this method of comparison persons contemplating marriage can learn beforehand whether or not they will make good partners. We found the book more entertaining than convincing.

Musik und Rasse.

By Richard Eichenauer. J. F. Lehmanns, Munich. 7.50 marks (paper); 9 marks (cloth). 6 x $8\frac{7}{8}$; 286; 1932.

Hitherto the science of music has made use of the concept of race only when treating the so-called exotic arts of primitive peoples. In the work of Eichenauer we have an interesting and stimulating attempt to interpret the origin, character and development of the musical art of the West, on the basis of the various racial strains that enter into the make-up of the diverse European populations. The thesis is that it is important and necessary both for the musician and the music-lover to obtain a thorough knowledge of the science of race for a full understanding and proper appreciation of this art. The book is amply illustrated with portraits of representative masters and musical notations from their works. It is also provided with a subject index and an index of names of composers.

Rassenkunde und Rassengeschichte der Menschheit. *Erste Lieferung (Bogen 1-9). Zweite Lieferung (Bogen 10-18).*

By Egon F. von Eickstedt. Ferdinand Enke, Stuttgart. 10 marks each Lieferung. $7\frac{1}{8}$ x $10\frac{1}{2}$; Lief. I, 144; Lief. II, 145–288; 1933.

The first two numbers of a series of six purposing to summarize the present-day knowledge concerning the biology and history of the races and racial mixtures of man. After a preliminary discussion, contained in *Lieferung* I, of anthropological methods used in studies of race and type, and a general account of the origin and development of man and the races of man, the material is treated by continents. The second number treats of the peoples inhabiting Asia, from anthropological and biodynamic viewpoints. These numbers are replete with photographs, diagrams, and maps. Indices for the set will appear in the final number. When completed, it is plain that this will be a notable addition to the literature of general anthropology.

The Family. *A Study of Member Rôles.*

By Katharine D. Lumpkin. University of North Carolina Press, Chapel Hill. \$2.50. $5\frac{1}{2}$ x $8\frac{1}{2}$; xix + 184; 1933.

This is a good book for the social worker

or those interested in sociological principles governing family life. Observations were made on forty-six families, clients of a family society in New York City. We are shown the endless variety of problems to be dealt with in family case work and offered excellent ideas on an approach to such matters as the various attitudes parents assume either to hide or to exaggerate a situation. We learn how the worker by understanding the main hidden motives behind an act can control a situation and build up a favorable attitude. There are also distinct family patterns, as for instance the wife who loyally assures the worker what a fine "provider" her husband has always been and in turn the husband who brags about what an excellent mother his wife is. However, with so much detail the reader has some difficulty in seeing the wood for the trees. There is an adequate index.

THE RACE BIOLOGY OF THE SWEDISH LAPPS. *Part I. General Survey. Prehistory. Demography. Future of the Lapps.*

With the Collaboration of the Staff of the Swedish State Institute for Race Biology and of K. B. Wiklund. Edited by H. Lundborg and S. Wahlund. Almquist and Wiksell, Uppsala; Gustav Fischer, Jena; G. E. Stechert, New York. Sw. Cr. 50 (Sweden); 50 marks (Germany); $15.00 (U. S. A.). $11\frac{1}{4}$ x 15; iv + 231; 1932 (paper).

This large monograph in folio represents the first volume of two on the Swedish Lapps to be published by the Swedish State Institute for Race Biology. Data for the study were derived largely from parish records covering approximately a century, from 1791 to 1890. Nearly one hundred pages of tabulated data give in detail all of the basic material used. The analysis is limited primarily to a comparison of the vital statistics and demographic characteristics of the two types of Lapps, the "nomadic" and "settled." The statistician for the Institute, Dr. S. Wahlund, furnishes an excellent and thoroughly sound evaluation of the errors inherent in the use of parish records. The general conclusions of the study are conservative and form a reliable and valuable contribution to the field of human biology.

TOLD AT THE EXPLORERS CLUB. *True Tales of Modern Exploration.*

Edited by Frederick A. Blossom. Albert and Charles Boni, New York. $3.50. $5\frac{7}{8}$ x 9; x + 425; 1931.

In spite of its considerable popularity, this symposium of contemporary travelers' tales cannot be regarded as a particularly notable or distinguished performance. Not only are the thirty odd chapters uneven in interest and treatment, as was to be expected, but some of the book is either rehashing or straight reprinting of already familiar stuff. Each chapter is prefaced by a thumb-nail biography of its author. The book is rather too sparsely illustrated with mainly excellent halftones. There is no index, an odd omission for this particular type of book. Its *raison d'être* is a worthy one—to make some money for the library of the Explorers Club.

FAKERS, OLD AND NEW. *A History of Cunning and Stupidity.*

By Maurice Chideckel. The Stratford Co., Boston. $2.00. $5\frac{3}{8}$ x $7\frac{7}{8}$; iii + 275; 1933.

Jazzy and superficial sketches of the gaudier religious imposters from Alexander of Aboniteichos to Alexander Dowie. For variety Mr. Chideckel mixes in a few murderers, literary forgers, pretenders, highwaymen and assorted rogues. The book is carelessly written. Thus the founder of the Catholic Apostolic Church appears as Irving Edwards. There is, of course, neither bibliography nor index. What might have been an interesting and valuable book becomes in Mr. Chideckel's hands merely a piece of cheap sensationalism. It seems a pity.

THE SKELETAL REMAINS OF EARLY MAN. *Smithsonian Miscellaneous Collections Volume 83.*

By Aleš Hrdlička. Smithsonian Institu-

tion, Washington. $2.25. $6\frac{1}{4} \times 9\frac{1}{2}$; x + 379 + 93 plates; 1930 (paper).

This accurate and very complete account of the known early skeletal remains of man will serve as a valuable reference work for all future anthropological investigation. Dr. Hrdlička has given in detail the history of each important find, its location and relation to other skeletal remains, and the geological formations of the region. Tables of measurements of all types are included and a chart showing the dimensions of teeth in early man. The volume is profusely illustrated with excellent photographs and drawings and is well documented and indexed.

SCIENCE AND HUMAN LIFE.

By J. B. S. Haldane. Harper and Bros., New York. $2.50. $5\frac{1}{2} \times 8$; viii + 287; 1933.

Dr. Haldane writes in his usual entertaining manner on a wide variety of subjects. As a sample we give the following: The scientific point of view; The inequality of man; Prehistory in the light of genetics; The place of science in western civilization; Physics declares its independence; My philosophy of life; What I think about; Birth control; Illnesses that make us healthier; and If Jesus lived today. The author's excuse for grouping these heterogeneous essays together is that a single idea permeated them, namely "How does science affect human life?" The volume lacks an index.

COMPENDIO STATISTICO ITALIANO, 1932-XI, *Vol. VI.*

Istituto-Centrale de Statistica del Regno d' Italia, Rome. $5\frac{1}{8} \times 7\frac{1}{4}$; 334; 1932 (paper).

Besides the usual presentation of Italian statistics, this number of the *Compendio* contains the results of the census of 1931, a chapter on the economic progress of Italy during the first decennium of the Facist regime, and an appendix on stillbirths and infant mortality. In spite of the Facist emphasis on procreation as a patriotic duty the birth rate has fallen even more rapidly during the past ten years than before. Unfortunately the book lacks an index.

ANTHROPOGEOGRAPHIE.

By Otto Maull. Walter de Gruyter & Co., Berlin. 1.62 marks. $4 \times 6\frac{1}{8}$; 136; 1932.

This little book of the well-known Göschen series gives an excellent concise account of the geography of man and his works. The author includes under anthropogeography demographic, racial, cultural, ethnographical and political factors. It is primarily intended for the general reader.

BULLETIN DER SCHWEIZERISCHEN GESELLSCHAFT FÜR ANTHROPOLOGIE UND ETHNOLOGIE. *(Bulletin de la Société Suisse d'Anthropologie et d'Ethnologie)* 1932/33, *9. Jahrgang.*

Société Suisse d'Anthropologie et d'Ethnologie, Zurich. 3 francs. $6\frac{1}{8} \times 9$; 59; 1933 (paper).

ZOÖLOGY

COLONY-FOUNDING AMONG ANTS. *With an Account of Some Primitive Australian Species.*

By William M. Wheeler. Harvard University Press, Cambridge. $2.00. $5\frac{3}{8} \times 7\frac{3}{4}$; viii + 179; 1933.

On a trip to Western Australia in 1931 Professor Wheeler was able to work out successfully the method of colony formation in the Ponerine ants. These insects, commonly known as the bull-dog ants, exhibit a hitherto unexpected method of colony founding which links the behavior of ants with that of the solitary and social wasps. After the nuptial flight, the queens of this type establish their colonies independently in single cells in the earth. These cells are sealed but in some of the forms the queen apparently emerges at intervals for the purpose of foraging for food and cleaning out the nest. This important finding concerning the behavior of an ancient and primitive type of ant has led the author to review and discuss in detail the independent method of colony formation among all

the ants. He stresses the importance and bearing which studies of typical behavior patterns have in the biological sciences. The volume contains numerous illustrations, a lengthy bibliography and an index.

THREE KINGDOMS OF INDO-CHINA.
By Harold J. Coolidge, Jr., and Theodore Roosevelt. Thomas Y. Crowell Co., New York. $3.00. $5\frac{3}{4}$ x $8\frac{3}{4}$; 331; 1933.

This is a narrative account of Kelly-Roosevelts Expedition to the northern part of French Indo-China and Szechuan for the purpose of collecting vertebrate material, and especially large mammals, for the Field Museum. The Expedition, like the book, fell into two parts, the one headed by Harold Coolidge, and the other by Theodore Roosevelt. The zoölogical booty garnered was rich and varied, and the country traversed extraordinarily interesting. Considering the difficulties of climate and country there was relatively little illness. This was evidently due to the knowledge, skill, and painstaking care taken by the Expedition's physician, Dr. Ralph Wheeler. Unfortunately the good record was marred by the death of one member, Russell Hendee, who contracted a particularly malignant form of malaria while travelling apart from the others.

The book is richly illustrated with excellent photographs, and a few line-cuts that entertain by their crudity. It will delight all who love travel and adventure, and contains much of interest to the anthropologist and ethnologist, as well as the zoölogist. It is well indexed.

ÉTUDE EXPÉRIMENTALE DE LA DIAPAUSE DES INSECTES. *Supplément XV au Bulletin Biologique de France et de Belgique.*
By Germaine Cousin. Laboratoire d'Évolution des Êtres organisés, Paris; Les Presses universitaires de France, Paris. 75 francs. $6\frac{1}{2}$ x 10; 341; 1932 (paper).

A description of a series of experiments on the nature of diapause in the various stages in an insect's life, its influence on the growth and metabolism of the insect and the effects of several factors, such as temperature, humidity, and light on the diapause. *Lucilia sericata* Meig. was used in most of the studies, but some experiments were also performed on other diptera—*Phormia groenlandica* Zett. and *Calliphora erythrocephala* Meig.—and the hymenopteron *Mormoniella vitripennis* Walk. Under conditions that were constant and optimal for the physiological equilibrium of the organism the author found continuous development to occur, and concludes that diapause is not a necessary episode in the life of insects. The bibliography covers 17 pages.

NATURE BY DAY.
By Arthur R. Thompson. Ivor Nicholson and Watson, London. 12s. 6d. net. $7\frac{1}{8}$ x $9\frac{1}{2}$; xi + 162; 1932.

There is as fine a collection of photographs of wild animals in this book as anyone could ask to see, not merely one picture of the representatives of a species, but often enough pictures so that one can get some notion of life history and habits. Most of his subjects (there are 122 photographs in all) are birds, but there is a very fair number of pictures of the smaller mammals, and of reptiles, fishes and insects. The text is a series of brief, informal sketches of the life histories of the diurnal British animals that an alert naturalist may hope to see, written for amateurs. There is no bibliography but there is a good index.

UP THE AMAZON AND OVER THE ANDES.
By Violet O. Cressy-Marcks. Hodder and Stoughton, London. 12s. 6d. net. $6\frac{1}{4}$ x $9\frac{1}{4}$; 337; 1932.

"I had still lots to see. This was Peru; the land of the Incas, the land of Pizarro. Also I must see a doctor, and then joy! there was my mail of six months." This is one scrappy sample only of a rather scrappy account of the author's journey up the Amazon and over the Andes. The lady can travel and keep a personal diary, but the reader might like some continuity of thought and the scholar better grammatical construction. There are some

good points to the book, however; one being many excellent illustrations and another some useful advice to the novice in exploration: "Don't try to load a mule with tin boxes . . . Don't take china or glassware. Don't take cooking pots unless you wish to use them yourself, as the natives will not use them." The appendices also include lists of camp equipment and scientific instruments. A little information about vampire bats and the fishes of the Amazon is given in the preface. There is no index.

DIAGRAMS AND SKETCHES OF SOME INSECT VECTORS *and Other Arthropoda Injurious to Man and Beast. For the Use of Students. Second Edition.*

By M. St. L. Simon. Garrett and Campbell, London. 4 shillings. $9\frac{1}{2}$ x $11\frac{1}{8}$; 9 folding plates; 1932.

A series of excellent diagrams and drawings designed for students of human and veterinary medicine, as well as of entomology. There are altogether eight plates, with an additional chart showing the different genera of insects covered in each plate. The purpose of the volume is to save much of the time the student spends in drawing and making lecture notes. There is plenty of room on each plate for the student to annotate, change or emphasize any aspects of the drawings. A useful pamphlet, embodying a pedagogical idea new to us, and worthy of consideration in other fields of zoölogy and botany.

THE ANIMALS CAME TO DRINK.

By Cherry Kearton. Robert M. McBride and Co., New York. \$2.50 net. $5\frac{1}{2}$ x $7\frac{3}{4}$; 219; 1933.

The author has spent 32 years in studying and photographing wild life in Africa. In this book he describes the "natural life of animals in Africa—particularly before that life is changed through the presence of the white man." An accurate observer, Mr. Kearton contributes much to our comprehension of what wild animals experience and endure in their natural habitat. It is unfortunate that his photographs have been so poorly reproduced. The book is without index.

TRAITÉ DE ZOOLOGIE. *Fascicule X et Dernier. Les Mammifères.*

By Edmond Perrier and Rémy Perrier. Masson et Cie., Paris. 45 francs. $6\frac{1}{2}$ x 10; 268; 1932 (paper).

Fascicule IV, on Birds, was reviewed in this journal in Volume VII, page 362. This volume follows the same plan as the previous ones, commencing with a general description of mammals, followed by a detailed discussion of their anatomy, physiology and morphology. The final section is devoted to a detailed classification of mammals. The present volume marks the completion of an excellent text and reference book.

A MANUAL OF FORAMINIFERA.

By J. J. Galloway. The Principia Press, Bloomington, Ind. \$6.50 (cloth); \$7.00 (buckram). $6\frac{1}{2}$ x $9\frac{3}{4}$; xii + 483; 1933.

A systematic description and classification of all known families, genera and species of Foraminifera, with an account of their distribution and habitats. This should be an exceedingly valuable reference work in micropaleontology.

AN ARCTIC SAFARI. *With Camera and Rifle in the Land of the Midnight Sun.*

By Richard L. Sutton, Richard L. Sutton, Jr., and Emmy Lou Sutton. C. V. Mosby Co., St. Louis. \$2.25. 6 x 9; 199; 1932.

This narrative of a hunting cruise along the coast of Spitsbergen contains much information on the habits of arctic birds, seals, walrus and polar bears. There are many excellent illustrations, an appendix on Spitsbergen place names and a bibliography but no index.

THE OCCURRENCE OF STREPTOSTYLY IN THE AMBRYSTOMIDAE. *University of California Publications in Zoölogy, Vol. 37, No. 17.*

By Theodore H. Eaton, Jr. University of California Press, Berkeley. 25 cents. $6\frac{3}{4}$ x $10\frac{1}{4}$; 6; 1933 (paper).

POSTJUVENAL MOLT AND THE APPEARANCE OF SEXUAL CHARACTERS OF PLUMAGE IN PHAINOPEPLA NITENS. *University of California Publications in Zoölogy, Volume 38, No. 13.*

By Alden H. Miller. University of California Press, Berkeley. 25 cents. $6\frac{3}{4}$ x $10\frac{1}{4}$; 22 + 2 plates; 1933 (paper).

BOTANY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung* 399. *Ernährung und Stoffwechsel der Pflanzen.* Containing following articles: *Physikalische Methoden der pflanzlichen Lichtphysiologie*, by Erich Nuernbergk; *Die Analyse von pflanzlichen Wachstumsvorgängen*, by Erich Nuernbergk and H. G. du Buy.

Urban und Schwarzenberg, Berlin. 15.50 R. M. 7 x 10; 275; 1932 (paper).

In the first section of this handbook the discussion of light filters of various kinds should be of interest to workers in a number of fields, in particular the description of the Christiansen filter in which the wave length of the transmitted light depends upon the temperature. There are also some notes of general interest on temperature and humidity control, photo-electric cells, thermopiles and other instruments for the measurement of temperature and light. The apparatus used by Nuernbergk and du Buy at Utrecht for measurement of the responses of seedlings in monochromatic light of low intensities is fully described. There are several chapters devoted to recent methods for study of reflection, absorption, and transmission of light, particularly the ultra-violet, in plant tissue.

The contents of the second section deal with motion picture equipment used for automatic registration of the behavior of seedlings stimulated by monochromatic light. There are devices for making quantitative measurements of the plant response as recorded on the film. Quite aside from its interest to specialists in light relations there are numerous ingenious devices for measuring this and that which should appeal to the mechanically-minded.

A BRIEF SKETCH OF THE LIFE AND WORKS OF AUGUSTIN GATTINGER.

By Henry N. Oakes. Cullom and Ghertner Co., Nashville, Tenn. \$2.00. 6 x $9\frac{1}{8}$; 152; 1932.

Augustin Gattinger was born in Munich, Bavaria, on February 3, 1825. His education for the degree of medicine was undertaken at the University, from which he was fired, however, in 1849, because of attendance at student demonstrations working for a more liberal government. In fact, he expressed his principles so strongly that he was forced to leave immediately for America. Whether or not he ever acquired the legal authority to practice medicine the author never clearly states. Anyhow, Dr. Gattinger settled first in Charleston and later in East Tennessee; he had in each place a rather large medical practice. Not long after he came to America he commenced his botanical researches upon which his fame largely rests. He was an ardent collector, and spent a large part of his time in the woods where he discovered many new species of plants.

The biography as a whole is rather disjointed and unevenly written. The last 75 pages, devoted to excerpts from Dr. Gattinger's correspondence with leading botanists of the day, is the most interesting part of the book. The old doc worked at his plants with an enthusiasm and thoroughness characteristically German.

DIE SPALTUNGSGESETZE DER BLÄTTER. *Eine Untersuchung über Teilung und Synthese der Anlagen. Organisation und Formbildung sowie über die Theorie der korrelativen Systeme. Beitrag XVI zur synthetischen Morphologie.*

By Martin Heidenhain. Gustav Fischer, Jena. 30 marks (paper); 32 marks (cloth). $6\frac{1}{2}$ x $9\frac{3}{4}$; xii + 424; 1932.

Unfortunately, this book was written about thirty years too late to receive the attention that is due it. This does not mean that it is not a good book; it is. It merely means that fashions in scientific thought have so changed since Heidenhain began his work that one does not often encounter now the dogma that the

cell is the only biological unit of structure, and this is the notion that Heidenhain set out to controvert. For him, cell groups, and even tissue cavities, are partly independent, self-regulating units, and when they divide they usually do so dichotomously. For leaves, which he can treat as planes and which are thus much more suitable than the salivary glands on which he began, he has worked out a simple numerical means for describing the division of leaves into lobes, and it must be said that his system works very well on even finely divided leaves. Taxonomists might do well to have a look at this part. He set out to bring animal and plant anatomy into a common ground, and he succeeded but his book is for philosophically inclined biologists.

RECHERCHES SUR LA RESPIRATION DES VÉGÉTAUX.

By Shri Ranjan. Imprimerie Régionale, Toulouse. 12 shillings. 6 x $9\frac{1}{2}$; 183 + 2 plates; 1932 (paper).

This is a thesis on the respiration of leaves. Ranjan is a former student of F. F. Blackman, and he has employed the experimental methods and the interpretations of his former teacher without making any essential changes in either. The section on anaerobic respiration is perhaps his best. Other sections deal with the influences of sugars, light and ozone. The whole book is characterized by the variety of methods and materials used rather than by thoroughness in any single part, but nevertheless his results deserve the attention of students of the subject.

FORTSCHRITTE DER BOTANIK. *Unter Zusammenarbeit mit mehreren Fachgenossen. Erster Band. Bericht über das Jahr 1931.*

Edited by Fritz von Wettstein. Julius Springer, Berlin. 18.80 marks. $6\frac{1}{2}$ x $9\frac{3}{4}$; vi + 263; 1932 (paper).

In treatment, this compilation stands midway between an abstracting journal and a textbook, and accordingly serves a very useful purpose. It is a collection of competently prepared, critical reviews of the botanical literature appearing during the year 1931, the several fields of botany being treated separately by specialists. It is proposed to issue further volumes annually, each covering one year's literature and they deserve to be widely read by botanists. There is no index, unfortunately; a bibliography follows each chapter.

MANUAL OF PLANT DISEASES. *Second Edition.*

By Frederick D. Heald. McGraw-Hill Book Co., New York. $7.50. $5\frac{3}{4}$ x 9; xii + 953; 1933.

The first edition of this standard text was noticed in Volume II, page 299 (1927) of this REVIEW. The important new researches since that time have been incorporated in this edition, especially those bearing on types chosen for detailed consideration. At the end of most chapters there is a list of important diseases, with references, which should be particularly valuable for the student.

WALDWEBEN. *Die Lebensgemeinschaft des deutschen Waldes in Bildern.*

By K. Gerhard and G. Wolff. Hugo Bermühler, Berlin-Lichtwefelde. 4.80 marks. $7\frac{3}{4}$ x 10; 128; no date.

In this beautiful book of photographs of the German forests, their trees and flowers, their mammals, birds, reptiles and insects, the authors aim to present the forest as a biological unit. The accompanying text is written with great charm. We can recommend the book to all nature lovers. There is an index.

TIETOJA METSÄNVILJELYS-TOIMINNASTA SUOMESSA, 1923–1930. *Silva Fennica 22.*

By Erkki K. Cajandas. Society of Forestry in Suomi (Finnland), Helsinki. $6\frac{1}{2}$ x $9\frac{5}{8}$; 35; 1932.

TUTKIMUKSIA KAASUTUHOISTA IMATRAN VALTIONPUISTOSSA. *Silva Fennica 23.*

By Esko Kangas. Society of Forestry in Suomi (Finnland), Helsinki. $6\frac{1}{2}$ x $9\frac{5}{8}$; 36 + 2 plates; 1932.

METSÄPATOLOGISEN TUTKIMUKSEN TEHTÄVISTÄ SUOMESSA. *Silva Fennica 24.*
By P. S. Tikka. Society of Forestry in Suomi (Finnland), Helsinki. $6\frac{1}{2} \times 9\frac{5}{8}$; 24; 1932.

EHDOTUS MAATALOUSYLIOPISTON PERUSTAMISEKSI (*Proposals for the Establishment of an Agricultural University*). *Silva Fennica 25.*
Society of Forestry in Suomi (Finnland), Helsinki. $6\frac{1}{2} \times 9\frac{5}{8}$; 94; 1932.

LAURI ILVESSALON MUISTO. *Silva Fennica 26.*
By Lauri Ilvessalo. Society of Forestry in Suomi (Finnland), Helsinki. $7 \times 9\frac{3}{4}$; 54; 1932.

ACTA FORESTALIA FENNICA 38. *Publications of the Society of Forestry in Suomi, Helsinki.*
$6\frac{3}{8} \times 9\frac{1}{2}$; 416; 1932.

CONTRIBUTIONS DU LABORATOIRE DE BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL. *No. 22: Études sur la Flore Algologique du Québec.—I.* by Jules Brunel. *No. 23: Contribution à l'Étude du Gentiana Victorinii*, by Jacques Rousseau.
Institut Botanique, Université de Montréal. 50 cents. 6×9; 26; 1932 (paper).

MORPHOLOGY

MORPHOLOGISCHE UNTERSUCHUNGEN AN DER FIBULA DES MENSCHEN UNTER BERÜCKSICHTIGUNG ANDERER PRIMATEN.
By Heinrich Sprecher. Orell Füssli, Zürich. $6\frac{3}{4} \times 9\frac{5}{8}$; 162 + 14 plates; 1932 (paper).

Measurements were made in this investigation from nearly 500 fibulae, from 18 different human races, 9 orang-outangs, 8 gorillas, 8 chimpanzees and 10 hylobates. The technique used for taking the measurements followed that in the texts of Martin and Gieseler. No definitive correlations came out of the study and the author says in conclusion that the fibula shows a multiplicity of shapes; that there is little racial differentiation; and that the fibula can be of but slight use for purposes of race diagnosis.

DISSECTION OF THE CAT. *Practical Directions for the Dissection of the Cat and the Study of Its Anatomy, to Accompany Reighard and Jennings' Anatomy of the Cat.*
By Jacob Reighard and H. S. Jennings. Revised, with the Addition of a Manual of Regional Dissection, by Rush Elliott. Henry Holt and Co., New York. $1.25. $5\frac{1}{2} \times 8\frac{1}{2}$; vi + 106 + folding chart; 1932.

A revision of the practical directions for cat dissection, first published by Reighard and Jennings in 1901, with the addition of a regional plan for dissection by Dr. Rush Elliott. It is hoped that the directions will prove more convenient for laboratory use in a separate booklet than they were before when incorporated in the *Anatomy*.

L'ŒUF HUMAIN ET SES ANNEXES.
By Maurice Lucien and Henri Vermelin. Gaston Doin et Cie, Paris. 35 francs. $6\frac{1}{4} \times 9\frac{5}{8}$; 157; 1933 (paper).

A useful concise manual, by the professors of anatomy and obstetrics at Nancy, for the student of obstetrics, summarizing the main features in the anatomy and physiology of human reproduction. It is clearly written, abundantly illustrated, and fairly well up-to-date, although some of the more recent American work is not adequately represented. It has neither index nor bibliography.

PHYSIOLOGY AND PATHOLOGY

THE NEURAL ENERGY CONSTANT. *A Study of the Bases of Consciousness.*
By John Bostock. George Allen and Unwin, London. 6 shillings net. $5\frac{1}{8} \times 7\frac{3}{4}$; 178; 1931.

It is impossible to give an adequate conception of the author's theories concerning the development of human consciousness and the neural energy constant in a few words. Primitive consciousness (in the single cell) he holds to be pure awareness of heat, cold, etc. Formation of slowly discharging cells (a center for emotion) linked up with the 'awareness center' came about for the need of avoiding extremes of temperature and simple dangers. Comfort and discomfort became associated with the centers and later paramount needs such as hunger and reproduction. Subsequent

elaboration of somatic tissues and complicated modes of life led to the development of the organ of fine adjustment or discrimination. "Complete consciousness occurs only when the three centers of awareness, emotions and fine adjustment are in correct functional apposition." The extreme fatiguability of the neuron (the basal structure for all nervous activity) is taken care of by the enormous numerical reserve of neurons which serve their turn as needed. The neural energy involved is a constant. The author applies his theory to an explanation of sleep, dreaming and mental diseases. The work concludes with a bibliography of 61 titles and an index. Sir John Macpherson contributes a foreword.

MALARIA. *The Governing Factor.*
By Elliot Fitzgibbon. C. W. Daniel Co., London. 5 shillings net. $5\frac{1}{8}$ x $7\frac{7}{8}$; 100; 1932.

Add one to the *Budget of Biological Paradoxes*. Like many another paradoxer the author writes with skill and subtlety, never letting the anti-vaccination and anti-vivisection cats out of the bag while he is writing about malaria. Indeed one very punditical journal reviewed the present volume in great seriousness, with all proper "on the one hand" and "on the other hand" stuff. The actuality of the matter is quickly set forth. The author, apparently a civil engineer who devotes a good deal of time and effort to maligning the art and science of medicine and its practitioners, is opposed to the idea that the mosquito is in any way involved in the epidemiology of malaria. His notion is that subsoil water is the real villain. We recommend the book heartily to teachers of epidemiology to put in the hands of their students as an exercise in detecting fallacious reasoning. It has no index, but nobody is likely to miss it.

LE RÔLE BIOLOGIQUE DE LA CATALASE DANS LE MÉTABOLISME D'ÉNERGIE.
By J. H. Regenbogen. Gaston Doin et Cie, Paris. 36 francs. $6\frac{1}{8}$ x $9\frac{1}{2}$; 139; 1932 (paper).

Regenbogen has a high respect for the properties of catalase.

In the metabolism of energy catalase performs the task of protecting the anaerobic phase and of putting a check on the aerobic. The function of the ferment is then directed toward the liberation and destruction of H_2O_2, formed and bound by the peroxydase and not toward the rejection of the free H_2O_2 present in traces in the cells to the degree which produces metabolism, thus purifying the cells of a cellular toxin, and providing them the necessary molecular oxygen for cellular respiration.

Starting from this his speculations take him over a large part of the field of respiration and enable him to propound a theory of the rôle of insulin in diabetes. Given encouragement, he says, he is sure he can trace the influence of catalase in arthritis, gout, obesity, arteriosclerosis, skin diseases, and cancer.

A STANDARD CLASSIFIED NOMENCLATURE OF DISEASE.
Compiled by The National Conference on Nomenclature of Disease. Edited by H. B. Logie. The Commonwealth Fund, New York. $3.50. $4\frac{3}{4}$ x $7\frac{1}{2}$; xvii + 702; 1933.

This nomenclature is the result of the collaboration between 27 national societies and governmental bureaus interested in medical, clinical and statistical projects, and the National Conference on Nomenclature of Disease. Previous nomenclatures have been considered in the development of this one which is more inclusive and takes into account both the etiology of the disease and the part of the body affected. The book is an effort to meet the need felt by many for a more accurate basis for mortality and morbidity statistics and for the recording of clinical results. The diseases are classified in a logical manner with the numbers of the International List of Causes of Death printed in italics for purposes of statistical comparison.

The book merits a good trial so that its faults, if any, may be corrected and an accepted standard nomenclature prevail.

CHEMICAL WAVE TRANSMISSION IN NERVE.
By A. V. Hill. The Macmillan Co., New York. $1.25. $5\frac{1}{4}$ x $8\frac{1}{2}$; ix + 74; 1932.

This lecture was delivered before a group of chemists at Cambridge in the hope

that a Chemist or two may be induced thereby to come to the aid of Physiologists in one of the most difficult—and therefore the most attractive—of all scientific problems, the nature of the change . . . which is transmitted in nerve.

The nature and properties of the nervous impulse are set forth clearly and in detail from the point of view of the physiologist; and the possibilities of further researches indicated, in which the author earnestly bespeaks the assistance of the chemist, the physicist and the engineer. In a group of appendices additional data are given on: (1) the excitation of nerve, (2) the measurement of the heat production of nerve, and (3) the energy of a nerve stimulus. The author includes a list of references and an index.

La Transfusion du Sang de Cadavre à l'Homme.

By Serge Judine. Masson et Cie, Paris. 24 francs. $6\frac{3}{8}$ x $9\frac{3}{8}$; iv + 145; 1933 (paper).

A clearly written account of a new surgical therapy. The author, prompted by Professor Schamoff's experiments with dogs, developed successfully the technique of substituting blood from cadavers for that of living donors in transfusion. The substitution presents no new difficulties for doctor or patient and is in many ways superior. The purity of the blood is assured by autopsy. One corpse yields enough for five to eight cases. The blood is easily conserved for more than fourteen days and consequently is ready for use at any time. In addition Professor Judine believes the blood of cadavers to have a sterilizing effect on the patient's blood that aids in fighting infection, causes a fall in temperature, and raises the tonus of the body.

The Organs of Internal Secretion. *Their Diseases and Therapeutic Application. With a Chapter on Obesity and its Treatment. Fourth Edition.*

By Ivo G. Cobb. William Wood and Co., Baltimore. $3.50. $5\frac{1}{2}$ x $8\frac{1}{2}$; xiii +303; 1933.

With the exception of the chapter on the Endocrine Glands and Nervous Disorders this book has been completely revised to take into account the important additions which have been made on the functions of the internal secretory organs since the third edition was published. Two chapters, one on Obesity and one on Infantilism, have been added.

The History of Dermatology.

By Wm. Allen Pusey. Charles C Thomas, Springfield, Ill. $3.00 postpaid. $5\frac{3}{4}$ x $8\frac{3}{4}$; xiii + 223; 1933.

This book represents a real contribution to the literature of medical history. It is a scholarly piece of work, covering developments in dermatology from the Egyptians to the present time. The author's outlook is broad and his literary style delightful. Besides a general index there is an historical index. There are excellent illustrations.

The Tides of Life. *The Endocrine Glands in Bodily Adjustment.*

By R. G. Hoskins. W. W. Norton and Co., New York. $3.50. $5\frac{1}{2}$ x $8\frac{1}{2}$; 352; 1933.

An authoritative, well written, up-to-date, popular account for the general reader of the high points of present day humoral physiology, illustrated, documented, and indexed.

BIOCHEMISTRY

Tissue Proliferation and Acid Base Equilibrium.

By Rudolf Bálint and Stefan Weiss. Translated by F. Morena with the assistance of G. C. Pether. Constable and Co., London. 18 shillings net. 6 x $9\frac{3}{4}$; ix + 211; 1932.

In Chapter I of this book, the problem of acid base equilibrium and its relation to inflammation in general is discussed, and the literature in the field briefly surveyed. Arguments in favor of the view that an important rôle is played by the displacement in the acid direction of the reaction of the blood and the tissues in the pathogenesis of ulcer are presented in Chapter II.

The other chapters of the book are concerned with the general connection existing between physiological and pathological processes and the regulation of the physicochemical reactions. The results of research into tuberculous inflammation, of tissue culture experiments *in vitro*, and of experiments on physiological and pathological growth all indicate that an acid reaction hinders, while an alkaline favors, all kinds of tissue proliferation. The book contains subject and name indices and a full bibliography.

HYDROCHEMISCHE METHODEN IN DER LIMNOLOGIE *mit besonderer Berücksichtigung der Verfahren von L. W. Winkler. Die Binnengewässer, Band XII.*

By Rezsö Maucha. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. 18 marks (paper); 19.50 marks (bound). $6\frac{5}{8}$ x 10; x + 173; 1932.

The quantitative chemical analysis of the waters of streams and lakes for ecological purposes has necessitated the development of a number of special methods which could be applied at the place where the samples were taken with simple apparatus in a minimum of time, and Winkler has been a leader in this kind of work. One of his students, Doctor Maucha, has compiled a well-written manual of analytical procedures of this type, well-indexed, and provided with nearly 150 literature references. The methods for measuring oxygen and carbon dioxide take up about half of the book, another section is devoted to the estimation of electrolytes, and the last part concerns dissolved organic substances.

SÄURE-BASEN-INDICATOREN. *Ihre Anwendung bei der colorimetrischen Bestimmung der Wasserstoffionenkonzentration. Gleichzeitig vierte Auflage von "Der Gebrauch von Farbindicatoren."*

By I. M. Kolthoff in coöperation with Harry Fischgold. Julius Springer, Berlin. 18.60 marks (paper); 19.80 marks (bound). $5\frac{1}{2}$ x $8\frac{3}{4}$; xi + 416 + folding plate; 1932.

A standard work by an authority in the field, revised and published under another title. The first two chapters, on the measurement of acidity, and the reaction of the ampholytes are essentially the same as in earlier editions. The chapter on the use of indicators in neutralization analysis has been omitted in this edition, as the author has treated this fully in his *Massanalyse*. The remainder of the book has been entirely rewritten and greatly expanded. Author and subject indices are provided.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 400. Allgemeine chemische Methoden. Die Methoden der Diensynthese.*

By Kurt Alder. Urban und Schwarzenberg, Berlin. 13.50 marks. 7 x 10; 212; 1933 (paper).

Organic compounds with two pairs of double-banded carbon atoms each may be made to combine by addition and this handbook contains many procedures of this kind. It is the last one of the series on general chemical methods and contains the index for the series.

EIN GANG DURCH BIOCHEMISCHE FORSCHUNGSARBEITEN.

By Arthur Stoll. Julius Springer, Berlin. 3 marks. $5\frac{5}{8}$ x $8\frac{1}{2}$; 41; 1933 (paper).

This review, which is based on a lecture read at a meeting of the *Vereinigung Schweizerischer Naturwissenschaftslehrer*, is limited primarily to discussions of recent contributions to the chemistry of chlorophyll, ergot, squill and some of their derivatives.

FILME UND FÄDEN. *Haupt-Vorträge. Gehalten auf der IX. Hauptversammlung der Kolloid-Gesellschaft in Mainz vom 28.–30. September 1932.*

Wo. Ostwald [Editor]. Theodor Steinkopff, Dresden and Leipzig. 12 marks. $7\frac{3}{4}$ x $10\frac{3}{4}$; 183; 1932 (paper).

A collection of the principal papers—with the exception of that by L. Michaelis, which will be published in a later number

of the *Kolloid-Zeitschrift*—presented at the 1932 meetings of the Kolloid-Gesellschaft. Those not originally presented in German have been translated.

SEX

SEX AND BIRTH CONTROL.
By Leon F. Whitney. $1.50. $4\frac{7}{8} \times 7\frac{3}{8}$; 71; 1932.

THE TECHNIQUE OF CONTRACEPTION. *An Outline.*
By Eric M. Matsner. 50 cents. $5\frac{7}{8} \times 8\frac{3}{4}$; 39; 1933 (paper).

What a people the Americans are! If a law is found to be inconvenient or unpleasant they promptly devise ways and means of getting around it. A combination of glad-hearted and naïve hypocrisy with great ingenuity of mind characterizes equally our attitudes towards such a simple and homely physiological matter as copulation, and such grave concerns as our foreign policy and the soundness of our currency.

There is a plethora of laws in this country forbidding or restricting the dissemination of birth control information to the lay public. But almost daily new books and pamphlets appear giving such information in ever greater detail and specificity. Mr. Whitney's book, written by a layman, and dedicated to "the Mothers and Fathers who will someday be the ancestors of a better America," has on the reverse of the page carrying the dedication, the following statement: "This book is for married people only. If you obtained a copy and you are unmarried, the agent who sold it to you violated the agreement with the publisher." Oh yeah! And then what?

Dr. Matsner's pamphlet is stated to be issued in response to a "demand from the medical profession," and as "a convenient summary for the busy physician," but, on the inside cover page the price is quoted at 20 cents a copy in "lots of ten copies," as against the single copy price of 50 cents. "Busy physician" my eye—in fact my singularly bilious eye!

The moral fervor of both of these treatises is high and noble; their physiology impeccable and fully illustrated. What more need we say. Under the law we are forbidden to state where or how either book may be obtained.

LOVE. *An Outspoken Guide to Happy Marriage.*
By X-Ray. The C. W. Daniel Co., London. 1s. net (paper); 2s. net (cloth). $4\frac{7}{8} \times 7\frac{1}{2}$; 55; 1932.

It was with relief that we read this simple, concrete exposition of the fundamental biological and psychological facts of sexual development. Unlike many of its kind, the book neither moralizes, nor enlarges on the "art" of love-making, nor sentimentalizes to a distressing degree. The viewpoint is that of sound mental hygiene. The book is not written for scientists, but should find a place in the hands of those with limited knowledge about the facts of sex.

BIOMETRY

STATISTICS *in Theory and Practice.*
By L. R. Connor. Isaac Pitman and Sons, New York. $3.75. $5\frac{3}{4} \times 8\frac{3}{4}$; xvi + 371; 1932.

This is a clearly and simply written introductory textbook. Part I, on statistical method, deals with the organization of a statistical inquiry, statistical data, statistical measurement, classification and tabulation, diagrams, graphs, derivative data, statistical groups, averages, dispersion, skewness, probability and error, sampling, correlation, index numbers, finite differences, interpolation, graduation and curve fitting. Part II deals with the sources of data for administrative, economic and business statistics and with practical applications of method. The value of the book is enhanced by a bibliography and an index.

LES PRÉLUDES ANTIQUES DE LA THÉORIE DES PROBABILITÉS.
By K. -G. Hagstroem. C. E. Fritzes, Stockholm. 6 kronor. $6\frac{1}{4} \times 9\frac{3}{4}$; 54 + 3 plates; 1932 (paper).

According to the historians of mathematics

the concept of mathematical probability dates back only to the fifteenth century. Hagstroem concludes, however, that the concept of degrees of probability which the Greek philosophers of the Sceptic school introduced foreshadowed the modern concept of subjective probability and that the Greek game of astragali shows, in the values assigned to different throws, a knowledge of their objective probabilities.

KÖRPERFORM UND LEISTUNG SECHZEHNJÄHRIGER LEHRLINGE UND MITTELSCHÜLER VON ZÜRICH. *Eine sozialanthropologische Untersuchung.*

By Ernst Biedermann. Orell Füssli, Zürich. $6\frac{3}{4} \times 9\frac{5}{8}$; 84; 1932 (paper).

Two hundred boys attending trade schools and the same number attending commercial schools, all between $15\frac{1}{2}$ and $16\frac{1}{2}$ years of age, are compared with respect to athletic performance tests and somatological characteristics. In general, the results are in accord with many similar studies of the differences between children whose parents fall in different socio-economic and occupational classes. An appendix gives all of the actual data on which the paper is based together with the statistical constants, mean, standard deviation, range and coefficient of variation.

MASS UND ZAHL IN DER PATHOLOGIE.

By Robert Roessle and Frédéric Roulet. Julius Springer, Berlin and Vienna. 16 marks (paper); 17.40 marks (bound). $6\frac{5}{8} \times 9\frac{5}{8}$; vii + 144; 1932.

The authors have summarized in this small volume a vast amount of numerical data on weights and measurements of normal organs and organ systems. The material is collected largely from the literature; tabulations are made specific for age and sex; and in general, the number of cases, the arithmetic mean, the standard deviation, and standard error of the mean are given. To those interested in quantitative pathology this is an invaluable handbook.

PSYCHOLOGY AND BEHAVIOR

CASE STUDIES IN THE PSYCHOPATHOLOGY OF CRIME. *Volume One, Cases I–V.*

By Ben Karpman. Mimeoform Press, Washington. $12.00 net. $8\frac{1}{4} \times 10\frac{1}{2}$; x + 1042; 1933.

The merit of this formidable treatise lies in its thoroughness. This becomes evident when it is perceived that 1039 solidly set large pages are devoted to the case-histories of *five* (only) individuals. Probably never before have psychiatric cases been reported (in print) with anything like such completeness of detail. The case material comes from the Department for Criminal Insane (Howard Hall) at St. Elizabeths Hospital. The purpose for which the colossal labor represented by the book was undertaken was "to gain an understanding of some problems of criminality through an intensive study of the lives of individual criminals, seeking particularly to uncover such psychogenetic factors as may be found behind the criminal reactions proper."

While the thoroughness of the work commands great respect the net results achieved seem hardly worth the trouble taken. The author attempts no general conclusions whatever. In essence the five cases come to about the following: Case 1 was a hypersensitive chap with an inferiority complex whose criminal behavior (never particularly important) arose from "overcompensation for a deep sense of defeat;" Case 2 belonged "to that class of drifters whose life is one long childhood;" Case 3 was a homosexual male prostitute who got caught in the practice of sodomy in the Army—*why* he was homosexual does not appear; Case 4 seems to have been just a jackass, without brains enough to keep out or get out of trouble however slight; finally Case 5 was able "to distinguish intellectually between right and wrong, but unable to choose the right thing emotionally."

In sum, Dr. Karpman appears to have succeeded in really understanding each of these five men, and the reasons for their individual difficulties. But, broadly speaking, what of it? Surely it is not a discovery to find that personalities defective neurologically or psychologically, or both, may inadvertently drift into crimi-

nality. Like Herbert Spencer and the horse race, 1039 pages of indubitably dull reading are not necessary to convince any sensible man of a conclusion so plain. In fairness it should be said, however, that the book will doubtless help to convince people that *punishment* offers no solution for such cases as these, either from the viewpoint of society or of the individual concerned.

The index of the book appears to us inadequate, even in spite of the author's defense of it.

MAGIC AND MIND.

By E. J. D. Radclyffe. The Macmillan Co., New York; A. and C. Black, London. \$1.00 (U.S.A.); 2s.6d. net (England). $4\frac{7}{8}$ x $7\frac{1}{4}$; 96; 1932.

We are accustomed, in our superior wisdom, to smile at the belief of the savage that his magic spells can bring rain or heal sickness. Yet, as Mr. Radclyffe points out, however mistaken the technique may have been, the conviction that man can control his environment is of vast importance. It is indeed the basis on which science and technology have been built up.

But unfortunately for mankind the road from magic to science was not a direct one. To learn the effective control of the environment is a long and difficult process. It is little wonder, therefore, that after the first stage of man's overcredulous conviction of his own powers there should have come a second stage when

> He began to believe himself a weakling and to become aware of great powers at work other than his own. He might have trusted them and been content; only too often he feared them, to the ruin of his peace of mind. He learned first uncertainty; then terror, guilt, and the sense of sin. He ceased to reverence himself, and wasted his reverence on others. He sacrificed his flocks, and even his children, his self-respect, and his manhood, to misconceived gods, his strength of body to power-loving kings, and his wits and confidence to mistaken priests.

In our relations with the physical world this stage is, in turn, passing. The physical sciences have given us a large measure of control over our external environment. But in our inner life and our relations with our fellow men the baneful influences of fear and taboo still linger. The author has hope of the development of a "science of living" which will not quarrel with our make-up and deny its exhibition but will have the courage of our nature, accept it, and arrange society around it.

THE SECRET OF LAUGHTER.

By Anthony M. Ludovici. The Viking Press, New York. \$1.75. $4\frac{3}{4}$ x $7\frac{1}{4}$; 134; 1933.

After a discussion of the various theories of laughter that have been proposed the author adopts as the basis of his own theory Hobbes's conclusion that "the passion of laughter is nothing else but *sudden glory* arising from some sudden *conception* of some *eminency* in ourselves, by *comparison* with the *infirmity* of others. . . . ." Laughter, for Mr. Ludovici, is the expression of superior adaptation; its origin is the baring of fangs by which animals warn off their foes. With the increasing use of external weapons the showing of teeth, while retaining its instinctive association, the expression of superior adaptation, was "transferred to all those manifold and complex situations in society in which gregarious animals either find or feel themselves superiorly adapted, or merely lay a false claim to such a position by means of bluff."

The craving for laughter of the present age is in Mr. Ludovici's eyes a symptom of its decadence. Mankind, oppressed by physical ills as well as by the complexity of the environment, resorts to the factitious and transitory superiority of laughter, instead of seeking to remedy its inferiority. Thus humor, like religion, plays the part of an opiate of the people.

This is a stimulating and provocative book. It is to be hoped that some of its inevitable opponents will accept the author's challenge to account for the facts by a theory as all-embracing as his. The book is well documented and contains an excellent index.

THE PRINCIPLES AND PRACTICE OF PSYCHIATRY.

By Alexander Cannon and Edmund D. T. Hayes. William Heinemann (Medical Books), London. 25 shillings net. $7\frac{1}{8}$ x $9\frac{3}{4}$; xvii + 437; 1933.

The authors of this book have had wide

experience in psychiatric work in English institutions. The purpose has been "to collect and to state in concise form the most recent knowledge in the realm of Psychiatry . . . . in a manner most convenient for teaching purposes, and for the preparing for the diplomas in Psychological Medicine of the various examining bodies." In the sixteen chapters hardly any phase of the subject of psychiatry has been neglected. This means that many topics are necessarily briefly treated. Nevertheless the book will serve exceedingly well those wishing to review the subject for examination. As a reference book physicians and lawyers will find it especially useful. The work contains many helpful diagrams and an appendix in which is collected much information which could not be conveniently included in the text. Unfortunately no bibliography has been included. Considering the extensive amount of material in the book the index seems hardly adequate.

THE PSYCHOLOGY OF ANIMALS *in Relation to Human Psychology*.

By F. Alverdes. Harcourt, Brace and Co., New York. $2.25. $5\frac{1}{2} \times 8\frac{1}{2}$; viii + 156; 1932.

Professor Alverdes contributes an interesting comparison of animal and human psychology to the field of popular scientific writing. The approach is essentially philosophical—that human beings are compelled to set up "fictions" in order to comprehend themselves and the world about them, that absolute knowledge is unattainable and only that knowledge can be attained which adapts itself to our sense organs and mental organization. The fiction is set up that, behind the whole life process, there is a psyche-like agent. Our consciousness would then be that region in which this agent is able to grasp itself. Since this is common to both man and animals mutual understanding is possible within limits. The limits depend on the fact that animal behavior is based on instinct whereas man is obliged to acquire by experience practically everything. As a rational contribution to a rather hackneyed but popular point of debate this book will interest the philosophically minded general reader.

WHAT WE PUT IN PRISON *and in Preventive and Rescue Homes*.

By G. W. Pailthorpe. Williams and Norgate, London. 5 shillings net. $4\frac{7}{8} \times 7\frac{1}{4}$; 159; 1932.

This little book can scarcely be disregarded by those who have the difficult problem of dealing with the asocial individual. The author bases her work on a study of the psychology of 200 female criminals and inmates in prisons and preventive and rescue homes in England. She stresses the following points in any attempt to deal with such cases:—criminals and asocial persons should be looked upon as individuals who are suffering from psychological illness or defect; the unconscious motive of the delinquent should be carefully considered; no real progress in psychological cases can be made unless the offender's coöperation is enlisted; and, finally, a better understanding of the neurotic motive which too often builds and drives the machinery of reform. A large part of the book is taken up with case histories. The final chapters deal with conclusions and suggestions. A brief bibliography is given, also an index.

INSECT BEHAVIOUR.

By Evelyn Cheesman. Philip Allan and Co., London. 4s. 6d. net. $4\frac{3}{4} \times 7\frac{1}{4}$; 189; 1932.

The argument which is developed in this book, somewhat obscurely and without careful discrimination between established fact and theory, is that insects live and move in a subconscious world of their own, comparable to the postulated human subconscious, and that there is progressive development of insects' mental faculties from the simplest to the highest. The latter, as judged by the author from their behavior, have reached the border between the subconscious and the conscious. Awareness of failure in attaining a goal, with change of behavior to more successful tactics, is taken to imply a state of consciousness and is regarded as inexplicable on the instinct theory alone. Examples are cited to illustrate the occurrence of this phenomenon. There is an index but no bibliography.

Behavior Mechanisms in Monkeys.
By Heinrich Klüver. University of Chicago Press, Chicago. $4.00. 6 x 9; xvii + 387; 1933.

This monograph presents the results of an intensive analytical study of the behavior mechanisms of monkeys. The viewpoint is primarily biological and foundations are laid for investigations of the neurophysiology of behavior. The author has devised valuable new techniques for use in experimentation. The results contribute to an exact knowledge of the perceptual world of an animal. The nature of the animal's perceptual organization is found to be surprisingly like that of man. There is a bibliography of 309 titles, and an index.

Ability in Social and Racial Classes. *Some Physiological Correlates.*
By Roland C. Davis. The Century Co., New York. $1.75. 6 x $8\frac{7}{8}$; xiv + 114; 1932.

The influence of biological variations on intelligence among social and racial classes is the problem discussed in this book. In order to avoid dispute over the nature of intelligence the author selected groups of people whose intellectual levels have been fairly well established by the standard intelligence tests. The groups investigated were white and negro college students, white and negro feebleminded, city white children, negro children, and mountain children. All groups were located in the South. Three biological phenomena were examined biometrically: (1) speed of nervous conduction as measured by the Achilles tendon reflex; (2) tapping rate; and (3) "electrical resistance of the body to a small current passing from the back of one wrist to the back of the other." This latter function, it is believed, corresponds rather closely to metabolic activity.

The author states in his summary that the study "may be said to have shown that certain biological variations are advantageous for the possession of good intelligence." A not altogether unforeseen conclusion.

Conditioning Finger Retraction to Visual Stimuli near the Absolute Threshold. *Comparative Psychology Monographs, Vol. 9, No. 3, Serial No. 43.*
By Sidney M. Newhall and Robert R. Sears. The Johns Hopkins Press, Baltimore. 75 cents. $6\frac{7}{8}$ x 10; 25; 1932 (paper).

A report of an experiment designed to determine absolute sensory thresholds simultaneously by two techniques, the conditioned response and the psychophysical judgment with the method of constant stimuli. Several definite results came out of the experiment, to wit: very low intensities of retinal illumination can be conditioned; also intensities which vary around a subject's absolute sensory threshold are conditionable; and "an established conditioned response can be as sensitive an indicator of sensory stimulation as a practical psychophysical judgment."

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

The Hilarious Universe. *Being Angela's Guide to Einstein—and That Crush.*
By Richard Dark. Basil Blackwell, Oxford. 4s. 6d. net. $4\frac{3}{4}$ x $7\frac{1}{4}$; 130; 1932.

This impudent treatise by the author of *Shakespeare—and That Crush* is dedicated "without permission but with the deepest respect" to the Astronomer Royal! Its alleged purpose is to supply a hypothetical child called Angela with the information necessary to pass the examination to get her G.G. astronomer's badge—G.G. meaning Girl Guide, the British equivalent to a Girl Scout. Dark writes the text and Derrick does the pictures. It is a ribald book they have made. It treats the history of ideas about cosmogony in an extremely disrespectful manner. Even Dr. Einstein, that wise and good man, is handled with ill-becoming levity. Students should not be permitted to read this book. Happily our sound and constructive professors will not care to read it. We try to be and believe that we are broad-minded and tolerant in our editorial work, but after all humor has its place, and that place is not to deride the very foundations of

science. If the words of Einstein, Eddington, Millikan, and Jeans—even their slightest words—are not to be held sacred and above profanation, then indeed is the underpinning of the Holy Temple of Science crumbling.

THE UNIVERSE OF SCIENCE.
By H. Levy. The Century Co., New York. \$2.00. 5 x 7¼; xiii + 224; 1933.

This book is a piquant instance of a mathematician reproving mathematics. The author, who occupies the chair of Mathematics at the Imperial College of Science, protests vigorously against certain fashionable tendencies in present day science. Such writers as Jeans, Eddington, Millikan and Smuts, he concludes, have "approached their problems against a background of outworn Idealist Philosophy none the less significant in its colouring because it has been unobtrusively though tacitly present." The cause of this tendencious idealism he finds in the dominance of the mathematician in experimental science, so that "Mathematical Physics, to many interpreters, has taken on the appearance almost of a separate science where facts about the world are *proved* rather than discovered by observation and experiment."

Levy's own viewpoint is naturalistic and inductive. The universe is not a tidy assembly of discrete entities but "an enormous interrelated dynamic muddle with intermittent patches of order and sanity." Man himself is not a detached intellect viewing the universe from an absolute point of vantage but an integral part of his environment, physical and social. In order to reach some measure of understanding we break up experience into isolated systems and deal with these separately. This is a necessary step but none the less dangerous. For we are always liable to forget that we have ourselves isolated these systems and to find something mysterious in the "emergence" of a molecule of water from the combination of atoms of oxygen and hydrogen.

This is a stimulating and clearly written treatment of the philosophy of science, which both the scientist and the layman will profit by reading. There is an index but no bibliography.

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THE QUARTERLY REVIEW *of* BIOLOGY

LOCATION OF THE TESTES AND BODY TEMPERATURE IN MAMMALS

By GEORGE B. WISLOCKI

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MOORE (1926, 1932) has advanced the hypothesis that the scrotum plays an important rôle in facilitating the maintenance of a temperature optimum for the production of spermatozoa. This hypothesis he has sought to substantiate by evidence of an experimental nature. He has shown in a variety of mammals that if the temperature of the testes is raised a few degrees, either by applying heat to them or by dislocating them into the inguinal canal or body cavity, spermatogenesis is interfered with or finally completely stopped. Recently Moore's observations have been confirmed and extended by the experimental work of Knaus (1932, a, b).

In view of Moore's observations, it lies close at hand to inquire as to whether in mammals there is a correlation between the body temperature of a given species and the fact that the testes may be located either intraabdominally or extraabdominally.

I thought it might be of interest in this connection to collect some of the widely scattered data on mammalian temperatures. It turns out that records for many orders of mammals are either absent or exceedingly fragmentary. Moreover, in view of the fact that some groups of mammals have an exceedingly unstable temperature regulation, the difficulty enters in of properly comparing their temperatures with those of the more stable groups. Some animals are, furthermore, subject to daily rhythms of slight range, whilst others are of wide range, and still others may show no discernible constant daily variation. Moreover, the peak of the daily curve may be diurnal or nocturnal, depending on the waking and sleeping states of the animal. In addition there is a large group of animals in which there are seasonal variations in temperature related apparently to a period of hibernation or torpor. Finally there are mammals which, although they do not hibernate, lead a sluggish existence, which fact may have a bearing upon the body temperature.

A delicate heat regulating center in the brain is believed to have developed in those animals whose body temperature remains fairly constant. Thus mammals

with little control over heat production and dissipation are thought to be primitive and more reptilian in this regard, whereas those whose control is stabilized are thought to have become more specialized. It will be of interest to see which groups of mammals fall into these two classes.

In spite of the meagreness of the data and the multiplicity of factors involved, it appears possible to arrive at a rough estimate of the prevalent temperatures of quite a number of mammals including some with and some without scrotal testes. The data in the literature are extremely helpful. To these have been added some observations of my own, as well as several sets of unpublished observations for which I am indebted to several of my colleagues, more particularly Drs. R. K. Enders and Frederick A. Gibbs. The temperature readings are expressed in centigrade throughout this paper. Unless otherwise mentioned, the temperatures were obtained by rectum.

OBSERVATIONS

The following groups of mammals have permanently intraabdominal testes:

- Monotremata: Echidnidae (spiny ant-eater), Ornithorhynchidae (duck-bill).
- Some Insectivora: Centetidae (tenrec), Macroscelididae (African jumping shrew), Chrysochloridae (golden mole).
- Xenarthra: Bradypodidae (sloth), Myrmecophagidae (ant-eater), Dasypodidae (armadillo).
- Proboscidea (elephant)
- Hyracoidea (cony)
- Sirenia (sea-cow)
- Cetacea (whale)

Of these mammals with permanently intraabdominal testes Weber (1928) sets the Cetacea and Dasypodidae (armadillo) apart by virtue of the fact that he believes they show evidence that the intraabdominal position of the testes is a secondary development, their ancestral forms having been mammals which possessed descended testes. Thus the apparently primitive condition in these animals is to be regarded as a secondary differentiation or reversion.

Of the orders with intraabdominal testes the only ones on which fairly adequate temperature records have been made are the Monotremata and the Xenarthra. Concerning the Proboscidea and the Cetacea there are a few isolated readings, whilst for the remaining orders there are no records. It would be especially interesting to have some observations on the insectivores, with and without descended testes, because they constitute a large and diversified group of extremely primitive mammals. Unfortunately those members of the Insectivora possessing abdominal testes are all tropical forms difficult to procure.

Monotremata

Echidna and *Ornithorhynchus* are believed from numerous considerations to be the most primitive mammals. Records of their body temperatures are fairly numerous. It will suffice for the present purposes to summarize the findings for these animals, quoting the more important papers and indicating the findings briefly.

Echidna:

- Average cloacal temperature, 29.4°. Sutherland (1897)
- Average cloacal temperature, 31.1°. Wood Jones (1923)
- Average summer animals, 30°–32.6°. Wardlaw. Cit. Wood Jones (1923)
- Average winter animals, 29.7°–32.3°. Wardlaw. Cit. Wood Jones (1923)
- Range of variation 22°–36.6°. Sutherland (1897) (See also Table 1.)

TABLE 1

Range of variation of temperature of Echidna according to Martin (1902)

AIR TEMPERATURE	RECTAL TEMPERATURE	LATITUDE	AIR TEMPERATURE	RECTAL TEMPERATURE	LATITUDE
4	25.5	9.3	5	27.6	12.4
10	27.3		10	30	
20	28.6		20	31.4	
30	30.9		30	33.4	
35	34.8		37	40	

Average temperature 28°–29° with environment at 15°. Martin (1902).

Ornithorhynchus:

Average for *Ornithorhynchus*, 32.2°. Wood Jones (1923)

Average for *Ornithorhynchus*, 30.3°. Burrell (1927) (See also Table 2.)

TABLE 2

Range of variation of temperature of Ornithorhynchus according to Martin (1902)

AIR TEMPERATURE	RECTAL TEMPERATURE	LATITUDE
5	31.8	3.5
10	32	
20	32.6	
32	33 6	
35	35.3	

Average temperature 29°–30° with environment at 15°. Martin (1902).

Monotremes:

Average for, 29.8°.

Air temperature, 15°. Martin (1902)

Xenarthra

To this group belong the sloths (Bradypodidae), ant-eaters (Myrmecophagidae) and armadillos (Dasypodidae), all of which possess undescended testes throughout life. The sloths are characterized by extreme sluggishness, the armadillos are active, burrowing mammals, while the ant-eaters are moderately active. According to Weber the armadillos have testes which are secondarily intraabdominal in that they exhibit anatomical evidence that their ancestors once had descended testes.

Our knowledge of the body temperatures of these groups of animals is recently acquired

Sloths. Bradypus tridactylus. Ozorio de Almeida and Branca de A. Fialho (1924). 14 observations with external temperature 19°–25.8°:

Maximum rectal temperature......... 32.9

Minimum rectal temperature.......... 30

Mean rectal temperature............. 32

Bradypus cuculliger cuculliger. Kredel (1928)

Range 27.7°–36.8°

Air temperature 24.5°–32.4°

Bradypus griseus griseus. F. A. Gibbs.

These observations have never been reported, so they will be given in some detail in Table 3. Two sloths at body temperatures of 33° (26° air temp.) were placed in a cold room and their rectal temperatures read over a period of hours.

TABLE 3

Temperatures of Bradypus griseus griseus

TEMPERATURE OF AIR	RECTAL TEMPERATURE OF Sloth 1	RECTAL TEMPERATURE OF Sloth 2	LENGTH OF PERIOD
26	33	33	0 min.
TEMPERATURE OF COLD ROOM			
14	32	31	12 min.
14	31	31	20 min.
13	30	29	45 min.
13	29	28	1 hr. 15 min.
12	28	27	1 hr. 40 min.
13	25	25	2 hrs. 40 min.
14	24	23	4 hrs. 50 min.
16	24	24	6 hrs. 15 min.
13	24	Animal died	9 hrs. 30 min.
12	23		11 hrs. 55 min.
Animal removed from cold room			
TEMPERATURE OF AIR			
26	23		0 min.
26	24		5 min.
26	26		10 min.
26	26		15 min.
26	27		20 min.
26	28		45 min.
26	29		1 hr. 50 min.

Ant-eaters. Tamandua tetradactyla. R. K. Enders
Air temperature, 26.1°.
Rectal temperature, 30°.

Armadillos.

Dasypus (Tatusia) novemcinctus. Ozorio de Almeida and Branca de A. Fialho (1924). 12 observations of rectal temp.: Mean, 34.4°; Max., 35.4°; Min., 33°.

Dasypus novemcinctus. Wislocki

No. 1. Cage temperature, 24°. Rectal temperature, 34.5°, female. Transferred to temperature of 5°.
1 hour at 5°, 33.5
2 hrs. at 5°, 32
3 hrs. at 5°, 31.5
4 hrs. at 5°, 30.5

No. 2. Cage temperature, 28°. Rectal temperature, 35°, male. Transferred to temperature of 0°.
1 hour at 0°, 34
2 hrs. at 0°, 31.5
3 hrs. at 0°, 30

No. 3. Cage temperature, 24°. Rectal temperature, 34.5°, male. Transferred to temperature of 19°.
1 hour at 19°, 33.5
2 hrs. at 19°, 33.5
3 hrs. at 19°, 33
4 hrs. at 19°, 33
5 hrs. at 19°, 32.5

No. 4. Cage temperature, 25°. Rectal temperature, 34.5°, female. Transferred to temperature of 21°.
1 hour at 21°, 33.5
2 hrs. at 21°, 33
3 hrs. at 21°, 32.5
4 hrs. at 21°, 32
5 hrs. at 21°, 31.5
6 hrs. at 21°, 31.5

No. 5. Cage temperature, 24°. Rectal temperature, 33°, male. Transferred to temperature of 11°.
1 hour at 11°, 32.5
2 hrs. at 11°, 31.5
3 hrs. at 11°, 30.5
4 hrs. at 11°, 29.5
5 hrs. at 11°, 29
Transferred to temperature of 21°.
½ hour at 21°, 30.5

No. 6. Cage temperature, 30°. Rectal temperature, 35°, female.
½ hour at 21°, 34.5
1 hour at 15°, 33.5
2 hrs. at 17°, 33
3 hrs. at 18°, 33
4 hrs. at 18°, 32.5
5 hrs. at 19°, 32.5

Brown (1909) gives several figures of temperatures of armadillos without mentioning the atmospheric temperature:

Dasypus sexcinctus, 32.2–34.1; *Dasypus novemcinctus*, 33.1–33.9.

Proboscidea

Records of temperatures on elephants are meagre but the few readings are fairly uniform.

Elephas indicus, old male, 35.7–36.4, Brown (1909)
Elephas indicus, old female, 36.2–36.4. Brown (1909)
Elephas indicus, young female, 35.8–36.6. Brown (1909)
Elephas indicus, 25 yr. old female, 36.2–36.7. Benedict-Fox and Baker Cit. Kanitz (1925)
Elephas oxytis, 15 yr. old male, 35.9. Benedict-Fox and Baker Cit. Kanitz (1925)

Cetacea

The records of whales are practically negligible. The readings are all from stranded individuals and in all likelihood do not represent the normal temperatures of these animals.

Cetacea. 36–37. Cit. Weber (1928)
Orca gladiator. 36.7. Portier. Cit. Kanitz (1925)
Tursiops truncatus. 36. Wislocki

It appears from these data that two groups of animals with undescended testes which have been investigated (the monotremes and the Xenarthra) have relatively low temperatures and extremely unstable heat regulating mechanisms. It is interesting that the heat regulation of the sloth is fully as unstable as that of *Echidna*. The data of Martin indicate that *Ornithorhynchus* possesses more stability than *Echidna*, whilst among the Xenarthra the armadillos appear to be somewhat less labile in their temperature fluctuations than the sloths. In regard to temperature regulation the Xenarthra appear to be fully as primitive as the monotremes.

The fact that these two groups of animals have intraabdominal testes is

somewhat indicative of a possible correlation such as Moore's hypothesis postulates, but is by no means proof of such a contention. The data for the elephant, another form with intraabdominal testes, indicate that this animal's temperature is lower than the average mammalian temperature, but it does not appear to be as low as those of either the monotremes or Xenarthra. Knowledge of the elephant's temperature regulation and its fluctuation applicable to the present discussion must await the accumulation of further observations. The data for cetaceans are also scarcely sufficient to be drawn into the discussion. Knowledge of the insectivores, an important group on which data are completely lacking, would add materially to the subject.

However, some further information may be gained by the reverse procedure, namely an investigation of the temperature of those groups of animals possessing descended testes. In this group the marsupials will be of extreme interest, since they are known to be in many respects primitive mammals, yet have testes which are descended.

TABLE 4

Classification of mammals with descended testes

	SUBINTEGUMENTAL	TRUE SCROTUM	PERMANENT DESCENSUS	PERIODIC DESCENSUS
Marsupialia	Phascolomyidae (wombats) Notoryctidae (marsupial moles)	Majority	All	None
Insectivora	Talpidae (moles) Soricidae (shrews) Solenodontidae (West Indies) Erinaceidae (hedge-hogs)	Tupaiidae (tree-shrews)	Tupaiidae	Talpidae Soricidae Solenodontidae Erinaceidae
Manidae (scaly ant-eaters)	All	None	All	None
Orycteropodidae (aard-varks)	All	None	None	All
Carnivora	Felidae Galidictinae (Madagascar) All Pinnepedia (seals, sea-lions, walrus)	Majority of Fissipedia	All	None
Ungulata	Rhinocerotidae Hippopotamidae Tapiridae (tapirs)	Majority	All	None
Rodentia	Some	Some	None	All
Chiroptera (bats)	None	All	None	All
Lemuroidea	None	All	All	None
Simiae	None	All	All	None

Mammals with descended testes are classified (Weber, 1928) according to whether they possess true scrotal sacs or not, and as to whether they have periodic or permanent descensus of the testes. A preliminary survey has convinced me that there is no clear cut correlation to be obtained, based upon the present data, between temperatures and the presence or absence of true scrotal

sacs (subintegumental or scrotal position of the testes). The question of periodic descensus of the testes will be touched upon later in so far as it applies to the discussion.

The mammals in which descensus of the testes occurs are arranged in Table 4.

Temperature records are lacking on the Manidae and Orycteropodidae, are scant on the Chiroptera and the Insectivora, but fairly abundant on representatives of all the other groups. Concerning one of the insectivores, *Erinaceus* (hedgehog), there are a few data by Pembrey (1903) which can be dismissed in a few words as far as the present discussion goes. *Erinaceus* undergoes hibernation and it was the temperature changes during the period of hibernation and awakening which were being investigated. However, in several animals kept in the laboratory and observed in the waking state during November and December the temperatures recorded next the skin of the abdomen ranged from 32 to 35. No statement is made by Pembrey as to the location of the testes in these animals; normally in the seasonal cycle of *Erinaceus* the testes are retracted into the abdomen by October and hibernation is about to commence. Consequently these temperature readings shed no light for the present purpose upon the relationship of body temperature to testes.

Marsupialia

Numerous observations exist on representatives of this order. No attempt will be made to quote them in detail; instead they will be summarized and the sources in the literature will be given.

Australian Marsupials.

The observations of Martin (1902) given in Table 5 are of considerable interest.

TABLE 5

Temperatures of Australian marsupials (Martin)

	AIR TEMPERATURE	BODY TEMPERATURE	LATITUDE
Dasyurus maculatus (native cat)	5	37.1	2.9
	10	37.1	
	20	36.6	
	30	38	
	35	40	
Bettongia (rat-kangaroo)	5	36.2	2.4
	22	36	
	30	36.2	
	40	38.6	
Trichosurus (Australian opossum)	5	36.1	1.7
	10	36.5	
	20	36.2	
	30	36.2	
	35	37.8	

Average for marsupials, 36.5 with environment at 15 (Martin).

Average 16 species of marsupials, 126 observations, 36, Sutherland (1897).

TABLE 6

Temperatures of Phascolarctos cinereus (koala) (Sutherland)

AIR TEMPERATURE	RECTAL TEMPERATURE
7.7	35
10	35.6
11.5	35.2
13.1	36
16	36.8
19	35.7
22	36
22	36.1
24.5	36.5

Phascolarctos cinereus (koala), 83 observations average 36.4, both sexes; males alone average 35.2 (Sutherland). (See also Table 6.)

Phascolomys lasiorhinus (wombat), 34.3 (single reading)

Phascolomys platyrrhinus, 34

Petaurus (flying squirrel), 5 observations, average 35.7

Dasyurus (native cat), 36 (single reading)

Phalangers (ring-tailed opossum), 22 observations average 36.6 (range 35–37 at 16.8–35 air temperature)

Phalangista vulpina, 36.1
Phalangista fuliginosa, 37.3
Kangaroos:
Macropus giganteus, 36.6 (single reading)
Halmaturus bennettii, 37.1 (single reading)
Petrogale xanthopus, 35.9 (single reading)
Dendrogalus grayi, 37 (single reading)

American Marsupials.

Selenka (1886) mentions that the body temperature of *Didelphys virginiana* is about 36.

Brown (1909) gives several observations placing the temperature of *Didelphys virginiana* between 32.7 and 34.7.

TABLE 7

Rectal temperatures of Didelphys marsupialis (didelphii). Gley and Ozorio de Almeida (1924). Air temperature, 20.2–24.2°

MEAN	MAXIMUM	MINIMUM
34.05	36.2	33
35.96	36.4	34.3
34.70	35.7	31.9

Average 33 observations, 34.6.

Johnson (1931) gives the temperature of an adult male opossum (*Didelphys virginiana?*) as ranging between 36.6 and 35.5 at a room temperature between 25 and 29 (5 observations). The same animal removed to a refrigerator temperature of 4 to 6 degrees showed a range of temperature varying from 33.5 to 34.7.

TABLE 8

Temperatures of Didelphys virginiana (Virginia opossum) (Wislocki)

AIR TEMPERATURE	RECTAL TEMPERATURE
14	32
17	33.5
17	34
18	33.5
20	34.5
23	34
26	33
26	34.5
26	34.5

TABLE 9

Temperatures of Didelphys marsupialis etensis

AIR TEMPERATURE	RECTAL TEMPERATURE	
26.7	34.9	(R. K. Enders)
26.7	34 6	(R. K. Enders)
29	36	(Wislocki)

TABLE 10

Temperatures of Marmosa mexicana isthmica (murine opossum) (Wislocki)

AIR TEMPERATURE	RECTAL TEMPERATURE
21 5	31 5
21.8	31.8
22	30 7
22	31.25
22	31.5
24	33 2
24.5	33 5
24.8	33
25.2	31
29	36
29	36 2

It will be seen from this brief survey that the temperatures of the marsupials are on the average considerably higher than those of the monotremes and the Xenarthra. The data also indicate that the new world Didelphyidae (*Didelphys* and *Marmosa*), considered by all systematists to be the most primitive of recent marsupials, possess lower body temperatures than the marsupials of the old world. The body temperatures of the former (*Didelphys* and *Marmosa*) taken alone do not differ as far as the present data allow one to draw a conclusion from those of the armadillos amongst the Xenarthra. Thus the body temperature of the animals (armadillos) possessing the highest average temperature in the group with abdominal testes is about the same as that of the animals (Didelphyidae) possessing the lowest average temperature amongst the marsupials which have descended testes.

Hence the separation of groups on the basis of temperature in association with descended or undescended testes is not sharp but one of degree only.

The majority of the groups of mammals with descended testes may be dealt with relatively briefly for the present purposes. I present here for a number of groups a summary of data collected by Kanitz (1925) whose work may be consulted for the detailed literature:

Ungulata:
- Sheep, 39–40 Minimum-Maximum
- Goat, 39–40 Mean
- Camel, 34.95–37.85 (A.M.–P.M.)
- Pig, 39.5 Mean
- Horse, 37.5 Mean

Rodentia:
- Rabbit, 38.7–40 Mean
- Rabbit, 37.5–41.6 (Air temperature 5–40)
- Guinea-pig, 38–39 Mean
- Rat { male, 32.1–36.5 (5–40 air temperature); female, 33.9–38 (5–40 air temperature) }
- *Coendou villosus*, 37.9 mean, 38.3 maximum, 37.3 minimum. Ozorio de Almeida and P. Galvao (1924)

The following data on hibernating rodents are of interest:

Ground-squirrels (*Citellus tridecimlineatus*)

The temperatures of ground-squirrels when not in hibernation according to Johnson (1931) range from about 32 to about 41, but a range of 35–39 is common in a warm room and of 31–36 in a cold room. The lower normal temperatures grade into those of slight torpor at about 29–32.

Prairie-dogs (*Cynomys ludovicianus*)

According to Johnson (1931) 57 daily records on five animals in a warm room showed a relatively stable temperature at 36–37, whereas 46 daily records on seven animals in a cold room ranged between 32 and 36. From these and other observations Johnson concludes that the prairie-dog hibernates only in the coldest weather.

Carnivora:
- Dog, 39 Mean
- Cat, 39.5 Mean
- Cat, 38.5–39.9 (Air temperature 5–40)
- Ferret, 39.3 Mean, 37.9–40.4 extremes. Cit. Pembrey (1898)
- Fur seal, 38.3 Mean. Hanna (1924)

It may be concluded from these figures that the majority of mammals with descended testes have relatively high body temperatures. Nevertheless amongst those rodents which do not hibernate the rat is conspicuous by possessing an unusually labile temperature. It is also noteworthy that male rats have lower average body temperatures than female rats. The question of sex differences in this regard is one to which relatively little attention has been paid. Sutherland (1897) makes a similar observation concerning the marsupial *Phascolarctos* (koala). He reports the average temperature of eighty-three observations as being 36.4. "However, females at the breeding season are always very decidedly above the ordinary degree of warmth. If such cases be excluded, the average is exactly 36. But the averages for males alone is only 35.2." Moreover according to Bormann, Brunnow and Savary (1923) lower temperatures in males than in females have been reported also for rabbits (Moore) and guinea-pigs (Lipschütz). In their own series of rabbits Bormann, Brunnow and Savary were unable to establish a sex difference in temperature, and they conclude that all previous claims of such differences are open to the criticism of faulty technique. Their argument of faulty technique does not, however, appear to me to explain adequately the fact that it is invariably in the males that the temperature is reported as being lower.

Chiroptera

The writer has had an opportunity to take the rectal temperatures of several tropical bats, which are given in Table 11.

Brief notes exist in the literature to the effect that the temperature of bats which are found in the hibernating state is very low, reaching the level almost of the atmosphere. However, in the non-hibernating season certain bats are reported to have body temperatures as high as 41 or 41.6 degrees (Johnson, 1931).

TABLE 11

Temperatures of bats

	AIR TEMPERATURE	RECTAL TEMPERATURE
Hemiderma perspicillatum aztecum	25 5	37 3
	26	36 4
	28 9	37 8
Phyllostomus hastatus panamensis	26	37

TABLE 12

Temperatures of Perodicticus potto (Wislocki)

AIR TEMPERATURE MID-DAY	RECTAL TEMPERATURE
27	35.2
28	37 6
29	37.8
30	37
31.5	36.7

Primates

The majority of observations upon the temperature of the Primates are of the Simiae, little account having been taken of the more primitive Prosimiae.

Prosimiae. I had the opportunity on several occasions of taking the rectal temperature of one of the Lorisinae, *Perodicticus potto*, given in Table 12.

The following observations on *Perodicticus potto* are given by Brown: 36.5; 36.2 (3 P.M.); 37.8 (11 P.M.).

For the Galaginae and Lemurinae the following temperatures are cited by Brown:

Galago crassicaudatus...... 37.1
Galago senegalensis........ 38.1
Lemur varius.............. 37.7–38.8 (July)
Lemur varius.............. 37.9–38 (April)
Galago senegalensis........ 36.2 (3 P.M.)
Galago senegalensis........ 37.8 (3 A.M.)

From composite readings of the temperatures of 22 lemurs, Fox (1923) places their temperatures at 38–39. Their diurnal fluctuations are reported as being irregular.

The Simiae have been the subjects of a number of observations:

Leontocebus geoffroyi, 36.7–40 Fox
Hapale jacchus, 38.8–39.2 2 obs. Brown
Nyctipithecus (Aotus) trivirgatus, 37.4–39.1 2 obs. Brown
Cebus, 37.6–39.1 Fox
Ateles, 37–38.9 Fox
Cercopithecus pygerythrus, 37.8–39.7 Many obs. Brown
Macacus, 37 6–39.1 Fox
Cercocebus, 37.2–39.2 Fox
Cynopithecus, 37.2–38.9 Fox
Papio, 37.6–38.9 Fox
Macacus rhesus, *Macacus rhesus*, *Macacus cynomolgus*, *Papio hamadryas*, *Cercopithecus patas*: Mean rectal, 38. Diurnal range 2–3. Many observations, Simpson and Galbraith (1906)
Macacus rhesus. Mean rectal, 38.2–38.6. Diurnal range, 2–4. Kanitz
Orang utan (*Simia satyrus*), 36.3–37.8 Fox
Chimpanzee (*Pan niger*), 36.3–37.8 Fox
Chimpanzee, 36.8–37.3 Low, high monthly mean during first year of life. Jacobsen, Jacobsen and Yoshioka (1932)
Man, 36.29–37.25 Minimum-Maximum. Diurnal range 1. Benedict and Carpenter. Cit. Kanitz.

It is apparent that the Primates, too, share the relatively high temperatures of the group of mammals with descended testes. It is of interest that the platyrrhine and catarrhine monkeys have on the average higher temperatures than man and that their temperatures are subject to a rather regular diurnal range that is much greater than that of man. Ac-

cording to Fox (1923) the anthropoid apes (orang utan and chimpanzee) have on the whole a mean temperature nearer the human than do the lower monkeys, but they present daily variations far greater than man. The gibbons, to quote the same observer, approach the monkeys in their mean temperatures and daily fluctuations.

The few figures for the Prosimiae indicate that their temperatures are on an average lower than those of the monkeys, approximating the level obtaining in man although there is apparent a tendency for rather wide and irregular fluctuation. No sharp difference is discernible between the body temperatures of the extremely sluggish lorises (*Perodicticus*) and the active Prosimiae (*Galago*, *Lemur*). In respect to sluggishness of life the lorises are comparable to the sloths amongst the Xenarthra and to the koalas amongst the marsupials. The extreme sluggishness of these groups of animals is not apparently linked with a consistently lowered body temperature. The sloths on the one hand have as low body temperatures as any mammal, the koalas and lorises on the other hand have temperatures which approximate fairly closely the temperatures of the more active members of the generic groups to which they belong. It may be, however, that further studies will show that the inactive lorises and koalas possess temperatures of an average level a degree or so below the active members of the groups to which they are related. Of the Australian marsupials, however, Sutherland cites the wombats and the flying-squirrels (*Petaurus*) as having the lowest averages, the sluggish koalas occupying third place.

DISCUSSION

The data presented in this paper do not deny a correlation between body temperature and the location of the testes. Indeed in the main they are favorable to an affirmative answer. Nevertheless it must be borne in mind that our knowledge of mammalian temperatures is on the whole so fragmentary that evidence damaging to such an assumption may arise upon further inquiry. In spite of this scepticism it can be stated that of those mammals with intraabdominal testes which have been fairly adequately investigated (*Echidna*, *Ornithorhynchus*, *Bradypus* and *Dasypus*) the body temperatures are far below the general average for mammals. Contrariwise the mammals with descended testes have, taken as a whole, relatively high body temperatures. The American marsupials exhibit the lowest body temperatures of the entire group with descended testes, their temperatures averaging around 32 to 35. It is difficult to reconcile this low average with Moore's hypothesis. The Australian marsupials, on the other hand, with averages ranging around 36–37 fit well into the group possessing descended testes. Should further data bear out the present indication that the elephant's temperature (undescended testes) is around 36, this would also require explanation to meet the hypothesis.

The occurrence of a periodic descent of the testes in certain hibernating mammals following a rise in body temperature upon awakening and at the onset of the rutting season would appear to be favorable to the hypothesis. According to accounts the body temperatures of hibernating mammals rise rapidly to a relatively constant level within a few hours or days after the termination of the period of dormancy. The body temperatures of those hibernating mammals belonging to the class with descended testes are as high, when not in hibernation, as the temperatures of non-hibernating

mammals with permanently descended testes. According to Johnson (1931), however, the fluctuations may be greater, for he found that the temperature of ground-squirrels when not in hibernation ranged from about 32–41 when subjected to cold and warm rooms. The temperatures of the marmot and woodchuck after awakening are given as around 37 (Dubois, 1896; Rasmussen, 1917). Shortly afterwards the testes descend and the rutting season ensues. In the hedgehog (*Erinaceus europaeus*), according to Marshall (1911), the testes remain descended from April until October coinciding with spermatogenesis and active accessory genital glands. During this period two litters may be born. In the woodchuck, on the other hand, from the account of Rasmussen (1917), the rutting season and the period of spermatogenesis are brief, occurring in April. The testes descend by April, but reascend by July remaining permanently in the abdomen throughout the summer, fall and winter. Excepting for the brief period of rutting, spermatogenesis is practically in abeyance during the remainder of the year. Only one litter is born. Sutherland Simpson (1911–12) took the temperatures of a number of woodchucks captured between July and December and found the temperature range to be between 34.6 and 38.6 with extreme readings from 33.6 to 41.2. Thus in the woodchuck the testes reascend into the abdomen in spite of a continued maintenance of high body temperature. The cessation of spermatogenesis in the reascended testes accords well with Moore's view. However, the temperature findings indicate that body temperature is not causally related to the ascent of the testes in this instance. It might be presumed from recent experiments with hormonal extracts that the anterior lobe of the hypophysis plays a significant rôle in the descent and ascent of the testes (Engle, 1932; Moore, 1932, p. 349). Although exposure of the testes to lowered temperature may be necessary for spermatogenesis to occur, the temperature influence is nevertheless only one of a number of factors playing a part in the complex cycle of events underlying periodic descent of the testes. Much more work needs obviously to be done upon the subject of periodic descent of the testes.

Leaving now the question as to whether Moore's hypothesis is borne out by the above findings, several other conclusions are deemed worthy of mention.

1. The lowest average body temperatures recorded in mammals are in *Echidna*. *Ornithorhynchus* and *Bradypus* (sloth) follow in second place with about equal averages and ranges. Next in order are the armadillos and the new world marsupials with approximately equal levels.

2. The new world marsupials (*Didelphys* and *Marmosa*) which have been investigated have a lower average temperature by several degrees than the Australian marsupials. This circumstance may be related to the fact that the new world forms are considered to be the more primitive.

3. A sluggish mode of life is not necessarily associated with a lower body temperature than those of closely related active genera. Three unrelated sluggish groups of animals are the lorises, sloths and Australian koalas. The lorises and koalas do not differ materially in body temperature from the respective groups of active animals to which they belong. The sloths on the other hand have markedly lower temperatures than the related armadillos. If a single reading may be taken as a slight indication, the fairly active ant-eater (*Tamandua*)—rectal temperature 30—shows closer similarity to the sloth than to the armadillo.

4. The Primates present interesting differences in their temperature regulation. The platyrrhine and catarrhine monkeys have higher temperature ranges than man and a greater degree of daily fluctuation. The Prosimiae exhibit a decidedly lower temperature range than the monkeys, but differing from that of man in the wide degree of fluctuation.

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SOME PROBLEMS OF THE ORIGIN, CIRCULATION AND ABSORPTION OF THE CEREBROSPINAL FLUID

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SINCE the discovery of cerebrospinal fluid in 1774 by Cotugno, a great amount of work has been directed to an understanding of the fluid. Yet many of its most elementary problems still receive dissenting answers and agreement today often exists only within the school of a particular investigator. Identical methods have frequently yielded various results and equivalent results have received diverse interpretations. A review must in consequence consider many points of view and risk being laborious and hypercritical in its effort to evaluate the worth of existing data.

This review is concerned largely with work done on the cerebrospinal fluid during the past ten years. Investigations of an earlier date have been discussed by Weed (1922). We shall consider here the sites of origin and escape of the fluid, its circulation and the so-called mes-ectodermal barrier between it and the blood. For discussions of the pressure of the cerebrospinal fluid, see the reviews by Weed (1922 and 1933).

THE SOURCES OF THE CEREBROSPINAL FLUID

Intraventricular Source

The occurrence of an internal hydrocephalus after obstruction of the aqueduct of Sylvius by pathological processes or experimental means has provided unequivocal evidence of an intraventricular source of cerebrospinal fluid. Investigation has been directed toward measuring the part played by the chorioid plexuses and the ventricular ependyma with the result that three views have been formulated: first, that the plexuses account for the major portion of the fluid and the ependyma only a relatively small increment; second, that the plexuses take no part in its production; third, that the ependymal cells are not concerned with fluid-formation.

Histological studies first directed attention towards the high columnar epithelial cells of the chorioid plexuses as a source of cerebrospinal fluid. Intracellular globules and granules were described and an attempt was made to correlate their relations with secretory activity. After critically reviewing the results of these investigations, Weed (1922), came to the conclusion that "there is no conclusive evidence that these intracellular structures constitute the intracellular mechanism for the elaboration of cerebrospinal fluid. The difficulty of final demonstration that these granules are discharged into the fluid or are in some way dissolved in that fluid, cannot at present be surmounted."

The last ten years have been without evidence which in any way weakens this conclusion. More recently Davis (1923–24) has studied the granules of the epithelial cells; on the basis of their reactions to fixatives and to stains, he decided that they are mitochondrial in nature and without a secretory rôle. It is consequently justifiable to state that histological studies

on the normal epithelial cells of the chorioid plexus have provided no evidence that these cells are concerned in the production of cerebrospinal fluid.

Evidence more difficult of evaluation has come from study of the chorioid plexus after administration of drugs and hypotonic solutions. It has long been known that, among other drugs, pilocarpine, ether and theobromine cause a striking increase in volume of the epithelial cells of the plexus. These elements double in height, most of the volume-increase coming from enlargement of the clear, vesicular, apical portion. Changes of the same sort, often to an even greater degree, have been reported by Weed (1923) following intravenous injections of hypotonic solutions. In these experiments with distilled water, the great increase of cell-size led to bulging, sometimes apparently to rupture, of the limiting membrane. There is no question, therefore, that hypotonic solutions and certain drugs lead to profound morphologic changes in the epithelial cells of the chorioid plexus.

Can these changes be accepted as evidence that the epithelial cells are concerned in the formation of cerebrospinal fluid? It has been thought, on the basis of inadequate and possibly misleading evidence (see Becht and Gunnar, 1921) that increase of cell-size is accompanied by an increased escape of fluid from the plexuses. Analyzing the morphologic changes produced by drugs, Becht (1920) contrasted the plexus cells with those of a typical gland such as the parotid. In the latter, increased activity is evidenced by reduction in size of the alveoli and the appearance of a clear zone at the base of the cells; in the former, supposedly increased activity is accompanied by increased size of the plexus cells which have a clear zone at their free ends. The implied criticism assumes an identity of secretion-processes in all types of gland-cells and because of the varied histological appearances of secretory activity cannot be relied upon. If it be agreed with Weed (1923), that the increased cell-size after intravenous hypotonic solutions is simply due to an intracellular accumulation of water and that the associated increase in cerebrospinal fluid pressure may be completely explained by an increase in brain-volume and intracranial blood-volume, we are again without evidence of new formation of cerebrospinal fluid. The data simply indicate that more fluid enters than leaves the cells without in any way demonstrating that fluid actually escapes from unruptured cells into the ventricle. The change is probably produced by passage of fluid from a medium of low osmotic pressure, the blood, to one of higher osmotic pressure, the epithelial cell. Here, then, are important observations which must at present go without final explanation. Accurate measurement of the rate of cerebrospinal fluid-formation with control of vascular reactions will aid greatly in an understanding of the cellular changes just discussed.

Certain observations have been made directly on the chorioid plexuses. Cushing (1914) reported that he saw fluid exuding from the plexus of a lateral ventricle in man; Howe (1929) made similar observations on experimental animals. Schaltenbrand and Putnam (1927) injected fluorescine intravenously, observed the plexus of the living animal with a microscope, and saw greenish fluid coming from the surface of the plexus. These results are all faced with the same objections—the plexus has in each instance been exposed to air and subjected to a pressure much below normal. That the arachnoid membrane "sweats" fluid under similar conditions is a rather common observation, but this is urged by no one as evidence of normal function.

In their important reports on experimental hydrocephalus, Dandy and Blackfan (1914) and Dandy (1919) offered evidence which seemed to them to be direct and conclusive. Because their results have been practically universally accepted as decisive, it is perhaps justifiable to discuss them in some detail.

Dandy (1919) described a unilateral hydrocephalus in dogs produced by occluding one foramen of Monro. He also found that if the foramen was blocked and the chorioid plexus removed at the same time, a collapsed ventricle resulted. As far as can be ascertained from the article, though a direct statement is lacking, this last kind of experiment was successful on only two animals. It was concluded that the plexus alone is responsible for the formation of cerebrospinal fluid.

In Dandy's experimental procedure, the foramina of Monro were plugged and the chorioid plexus removed through transcortical incisions. It is quite obvious that such an operation, even in the most skilful hands, is delicate and difficult, and calls for clear demonstration that its aims have been fully realized. It must first have been certain, at the end of the experiment that the foramina of Monro were so completely blocked as to make escape of fluid impossible. Dandy apparently relied solely on macroscopic inspection, since no mention was made of microscopic examination or demonstration (for example, with a colored solution) that the block between the ventricles was complete. The dilatation of the ventricle with intact plexus is not to be regarded as an adequate control. There was the further necessity of demonstrating microscopically that there was no possible escape of fluid through the healed transcortical incision from the ventricle directly into the subarachnoid space; figure 7 of the 1919 communication indicates that this was not altogether improbable. And this demonstration must include evidence that the ventricular ependyma at the site of the wound was intact; otherwise fluid might well have passed from the ventricle into the substance of the brain. Any one of these three objections, if valid, would appear to impair the conclusions drawn from the experiment.

It is rather difficult, moreover, to be certain that the chorioid plexus was completely removed from the lateral ventricle. Describing the operation in which the aqueduct of Sylvius was occluded and the chorioid plexuses of both lateral ventricles extirpated, Dandy and Blackfan (1914) stated: ". . . . a good exposure of the entire lateral ventricle was obtained and the choroid plexus almost completely extirpated." Again: "An internal hydrocephalus had resulted from the occlusion placed in the aqueduct of Sylvius thirty-five days previously, *in spite of the almost complete bilateral extirpation of the choroid plexuses of the lateral ventricles.*" The italics are those of Dandy and Blackfan. Five years later, describing the same experiment (this is evident from the illustrations), Dandy (1919) stated: " . . . . the choroid plexus of both lateral ventricles was removed. . . . . The accumulated cerebrospinal fluid forms *solely* from the choroid plexus of the third ventricle." Here, then, is a discrepancy which may be important. Description of an experiment in 1914 states that the plexus was *almost* completely extirpated; in 1919 it is to be inferred that in the same experiment, and in others involving the same operative procedures, plexectomy was *complete.* Though Dandy's work may be fully substantiated in the future, at present his conclusions appear acceptable only with reservations.

Some collateral but not direct evidence suggesting that the chorioid plexus is con-

cerned in the formation of cerebrospinal fluid has come from embryological studies. Weed (1917), in embryo pigs, noted that the first extraventricular spread of cerebrospinal fluid is correlated with beginning tufting of the plexus. The same picture was found in *Amblystoma punctatum* by Flexner (1929). He also noted that in every instance brain transplanted from several of these embryos to the brachial or flank region of other *Amblystoma* developed chorioid plexuses and ventricles which were sealed off at their ends. After about two months in the hosts, several of these transplants were distended into great, thin-walled cysts filled with fluid. Similar transplants of spinal cord, in which fluid-formation would have to occur without chorioid plexus, were never dilated to this degree. These findings are offered simply as suggestive evidence that the plexus is in some way responsible for production of cerebrospinal fluid.

Relatively few investigators have dissented from the opinion that the plexuses have to do with fluid-formation. Among those disagreeing is Coupin (1930) who reported studies on fish. He pointed out that the meningeal space in ganoids and cyclostomes lacks fluid but instead is filled with adipose or myxomatous tissue. Chorioid plexuses, however, are present and particularly well developed in the cyclostomes. The apparently complete absence of cerebrospinal fluid in the presence of apparently well-developed plexuses led Coupin to the general conclusion that the two are in no way related—certainly an assumption not to be carried to other animal forms without many reservations. He is in part answered by Kappers (1926), who found that fluid is lacking in the leptomeningeal spaces, but that there is good evidence of its presence within the ventricles. All these investigations on fish have been made on fixed material in which the demonstration of cerebrospinal fluid is uncertain, perhaps impossible. It is not yet finally determined, therefore, whether extraventricular fluid is lacking in ganoids and cyclostomes. The "meningeal space" filled with adipose or myxomatous tissue may be homologous with the epidural space of mammals which also contains adipose tissue. If this be true, the "meningeal space" of fish should not be confused with the subarachnoid space of mammals.

Having noted in cases of ventricular hemorrhage that the epithelial cells of the chorioid plexus contained hemosiderin granules, Askanazy (1914) suggested that the plexus might be concerned in the absorption of cerebrospinal fluid. Hassin, Isaacs and Cottle (1922) and Wüllenweber (1924), corroborating these findings, stated that they are to be taken as definite evidence of absorption by the plexus. Klestadt (1915) injected carmine, fat and glycogen into the ventricle, found them all in the epithelial cells of the plexus, and so concluded that cerebrospinal fluid was being absorbed. These views, very briefly outlined here, find their extreme expression in Hassin (1930a and several other papers) who, on the basis of these observations and highly questionable pathological findings, concluded that the chorioid plexus absorbs certain constituents of the cerebrospinal fluid and assumed that it is not concerned with its formation. It seems highly probable that these conclusions are unwarranted, that the observations mentioned are not associated with absorption of cerebrospinal fluid but are to be related to phagocytosis and to the same sort of cellular activity which accounts for the storage of vital dyes.

The contribution made by the ependymal cells to the ventricular fluid is difficult to measure and few data have been offered to a solution of the problem. On

the basis of the experiments discussed above, Dandy (1919) concluded that the ependyma takes no part in its formation. Wislocki and Putnam (1924) sacrificed animals about an hour after intravenous injection of potassium ferrocyanide and iron ammonium citrate; after proper fixation, Prussian Blue granules were found in the ependymal cells of the areae postremae at the caudal end of the fourth ventricle. It was consequently suggested that the ependymal cells of these areae made a small addition to the ventricular fluid. Weed (1917), finding evidences of fluid in the ventricles of pig and human embryos before the appearance of the chorioid plexus, concluded that in embryos at least the ependymal cells take part in fluid production. Corroboratory evidence was found in transplants of the spinal cord of *Amblystoma* by Flexner (1929). In some of these transplants the central canal was small, but in others high, columnar ependyma was correlated with formation of fluid-cavities about as large as the fourth ventricle of the normal embryo. Finally, by microscopic examinations done in much the same way as those on the living chorioid plexus, Magnus and Jacobi (1925) found evidence of fluid coming from the ependymal cells.

It is evident from the foregoing discussion that we lack exact evidence of the sources of the intraventricular fluid. No experiment has as yet been devised to give an unequivocal answer to the problem. Despite the weakness of our data, however, it is probably justifiable to work with the hypothesis that the chorioid plexuses make the major contribution to the fluid. Their high vascularity, great surface area and the weight of experimental evidence speak in favor of this assumption. In the same unsatisfactory way, it is to be supposed that the ependyma adds a relatively small amount of fluid to that elaborated by the plexus. Our foundation for quantitative statements is so inadequate, however, that it would furnish little challenge to valid contradictory observations.

Extraventricular Sources

The history of the development of our present views on the histology and physiology of the perivascular spaces of the central nervous system has recently been presented by Schaltenbrand and Bailey (1928). The very brief account to be given here of the opinions of early investigators is taken almost entirely from their article.

The spaces about the blood vessels of the brain were first described by Pestalozzi (1849). Subsequently Virchow (1851), Robin (1859), His (1865) and Roth (1869) made contributions to the subject but the first description agreeing fairly closely with that now rather generally accepted came from Key and Retzius (1876). These last investigators believed that the blood vessels, piercing the leptomeninges and subarachnoid space to dip into the brain, carried with them a visceral endothelial cellular layer corresponding to the arachnoid membrane and a parietal layer of endothelial cells corresponding to the pia mater. The space between these two layers of endothelial cells was designated the perivascular space. The processes of glial cells were said to be in intimate connection with the cerebral side of the vascular pia. The parietal wall of the perivascular space might consequently be looked upon as a pial-glial membrane. Held (1909) largely agreed with this view and it has since been accepted in its essentials by Cushing (1925), Weed (1914) and others. Spielmeyer (1922), however, has questioned the conclusion that the perivascular spaces constitute true fluid-channels in the brain and is of the opinion that only indeterminate spaces are present

within the loose tissue of the adventitia of the blood vessels.

The problem has more recently been reinvestigated by Schaltenbrand and Bailey (1928). They concluded that the perivascular spaces around the larger vessels are bounded by two connective tissue layers corresponding to the pia and arachnoid or lie in a loose connective tissue of leptomeningeal origin and not to be split into layers. This is a view very similar to that of Key and Retzius. The tissue about the smaller vessels is said to be derived from the pia and lies either apposed to the muscularis or the endothelium of the vessel.

Several investigators (see Essick, 1920), using a method of silver staining, have found in the central nervous system the same picture of fluid-spaces lined by mesothelial cells as originally given by Key and Retzius. Schaltenbrand and Bailey, however, were unable with silver stains to demonstrate except rarely a layer of endothelial-like cells either in the subarachnoid or perivascular spaces. All the cells seen in their preparations gave rise to fibers, though the fibroblasts of the pia next to the spaces were often found to be somewhat flattened. They consequently inferred that the leptomeninges are without a layer of endothelial cells. An equivalent observation was made by Mallory (1920) in the subarachnoid space. Vital staining of the meninges, in the hands of Woollard (1924) and Kubie and Schultz (1925) has led to the identification of arachnoid lining cells thought to be truly mesothelial and so distinct from fibroblasts. The irregularity of results obtained with the silver technique might consequently be considered unimportant in view of the findings with the method of vital staining. Those investigators who have failed to find mesothelium lining the subarachnoid or perivascular spaces have been so positive in their identification of fibroblasts, however, and the nature of the cell-type lining these fluid-spaces is so important to an understanding of the permeability of the lepto-meninges, that it seems well to leave the question open for future work. It seems proper, nevertheless, to add that the weight of evidence favors the view that mesothelial cells line the extraventricular pathways of the cerebrospinal fluid.

The cerebral side of the pia was found closely opposed to a glial membrane, the Limitans glia, by Schaltenbrand and Bailey. Astrocytes were seen to send their foot-plates down to the pial membrane in such a way that in all vessels, except possibly capillaries, glia and pia together formed an uninterrupted membrane. His' space, thought to lie between glial and pial cells, was consequently judged to be an artifact.

His in 1865 was the first to demonstrate those spaces about the nerve cells of the brain called pericellular or perineuronal spaces. Mott (1910) made an important contribution while studying experimental cerebral anemia when he found that these spaces open into the perivascular spaces. Evidence in substantiation of Mott's pathway came from Goldmann's (1913) injection of spaces about the ganglion cells with trypan blue introduced into the subarachnoid space. Using a moderately elevated pressure in the subarachnoid space, or after cerebral anemia caused by ligation of the arteries in the neck, Weed (1914) was also able to inject the perineuronal spaces via the perivascular spaces with the Prussian blue reagents. Weed followed Prussian blue granules through pericapillary spaces. A leptomeningeal sheath was also seen by Schaltenbrand and Bailey about the capillaries, but, unlike the larger vessels, there was no lumen between the sheath and the vessel wall.

The experiments of Mott on cerebral anemia led him to the view that cerebrospinal fluid flows normally from the subarachnoid spaces through the perivascular spaces to the pericapillary or perivenular spaces. This is a view which today has been abandoned. The old experiments of Spina (1899) in which drops of fluid were seen on the surface of a brain prolapsed after production of an experimental hypertension are against this view. Recently Magnus and Jacobi (1925), observing the surface of the brain with a microscope, obtained much the same results as gotten by Spina. The most significant evidence against Mott's view, however, has been given by Weed (1914). He irrigated the subarachnoid space for several hours at normal pressures with the Prussian blue reagents and failed to find the reagents in the perivascular spaces. He concluded, therefore, that flow in these spaces is seemingly towards, not away from, the subarachnoid space.

It appears probable, then, on the basis of the best available observations, that there is a remarkably definitive fluid-pathway from the neurones to the subarachnoid space. Around each neurone, in the present view, is a minute or "potential" perineuronal space, probably equivalent to the tissue spaces of other organs, which communicates with the loose connective tissue around a capillary. The pericapillary tissue in turn leads into the larger perivascular space. The visceral wall of this space is formed by cells carried down from the arachnoid membrane. The parietal wall is composed of pial cells and the prolongations of astrocytes in intimate connection with the fibroblasts of the pia. Doubt exists as to whether the space is lined by an endothelium or mesothelium or by slightly differentiated fibroblasts.

One more important question remains to be discussed. Is it possible to gain a measure of the amount of fluid flowing from the perivascular spaces to the subarachnoid space? In a review, Weed (1922) concluded that "the perivascular spaces . . . . pour a certain amount of fluid into the subarachnoid space, where this fluid mixes with the liquid produced in the cerebral ventricles." As is also noted by Weed (1914), "the space about the nerve cells is probably chiefly potential in character, filled during life by a very thin layer of fluid." Schaltenbrand (1928) has concluded that a stream of cerebrospinal fluid from the perivascular spaces to the subarachnoid space is not definitely disproved but appears to be unlikely. This opinion is based on evidence from two sources. Having injected fluorescine intravenously, Schaltenbrand and Putnam (1927) observed the surface of the brain of the living animal with a microscope and failed to see any escape of dye such as might be anticipated were there fluid flowing from the perivascular spaces. In their histological studies on normal brains, Schaltenbrand and Bailey (1928) noted the absence of a true space about the capillaries and smaller vessels. In another effort to test the view that there is a fluid-stream from the perivascular spaces, these investigators studied the size of the spaces after disease or experimental procedure had supposedly occluded the subarachnoid space. The finding of spaces of apparently normal size in such cases appeared to them to substantiate the conclusion that a circulation of perivascular fluid under normal conditions is improbable. As far as can be judged from the description of their experiments, however, there is no clear evidence that they were dealing with complete occlusion of a part of the subarachnoid space.

As will be discussed later in considering the circulation of the cerebrospinal fluid, the amount of fluid flowing from the

ventricles is small. In the cat it appears that only about 0.6 cc. per hour flows into the subarachnoid space from the ventricles. In view of their great numbers, it is apparent that all the perivascular spaces may make a small but significant contribution to the fluid in the subarachnoid space though the amount of fluid leaving any particular space be minute. The evidence at hand does not appear to controvert this view. The perivascular spaces, as will be discussed later, are perhaps best to be regarded as an accessory pathway for drainage of the tissue-fluid of the central nervous system. They are in this sense analogous to the lymphatics of other organs. If drainage from them be interrupted, as for example may happen in experimental occlusion of the subarachnoid space, compensation may be anticipated through increased absorption by the venules. The lack of a true space in the loose tissue around the capillaries and smaller blood vessels, and the presence of a true space filled with fluid around the larger vessels, is compatible with the view that the capacity about a stem-vessel must be large in order to receive the very small amounts of fluid present about each of its many branches.

It appears certain that under normal conditions no more than very small amounts of fluid pass into the subarachnoid space from a single perivascular space. The evidence at hand makes it difficult to add any exactness to this very unsatisfactory statement. It may be added, however, that it is not unreasonable to suppose that normally there is a very sluggish, probably irregular or interrupted, movement of fluid from the perivascular spaces to the subarachnoid space. The presence of fluid in the spaces about the larger vessels speaks in favor of this opinion. So too do the observations of Kubie and Schultz (1925). Having given hypotonic solutions intravenously, they found evidence of a definitive fluid-stream in the perivascular spaces, leucocytes lying in these spaces being "washed out" into the subarachnoid space. It appears reasonable, therefore, to assume that by decreasing the osmotic pressure of the blood, they simply magnified a very slow movement of fluid which normally takes place.

That certain of the constituents of the cerebrospinal fluid vary in their concentrations at different levels of the central nervous system is well established. The protein of the fluid, for example, increases in concentration from the ventricles to the lowest portions of the subarachnoid space whereas the glucose is in slightly greater concentration within the ventricles. This variation in concentration has been explained by some on the basis of admixture of perivascular fluid, relatively rich in protein and poor in sugar, with fluid from the ventricles and has been given as suggestive evidence of flow from the perivascular spaces. Other explanations, perhaps less satisfactory, suggest themselves for these findings. It is possible that the water of the cerebrospinal fluid is more rapidly absorbed than is the protein and that consequently fluid furthest removed from its source is richest in protein. A diminution in the concentration of sugar may perhaps be due to its use by the cells lining the subarachnoid space. The supposition is made by some that these differences in chemical constitution arise because of admixture of fluid which seeps through the walls of the blood vessels traversing the subarachnoid space.

There is a little evidence suggesting that cerebrospinal fluid arises from the blood vessels within the subarachnoid space. After intravenous injections of urea and sodium salicylate, Cestan, Laborde and Riser (1925) found equivalent concentrations of these substances at different levels

of the subarachnoid space after about twenty minutes. The same results were obtained after isolating the lower subarachnoid space from the ventricles by ligature. The permeability of the vessels of the subarachnoid space to the dye fluorescine has also been studied. After injecting it intravenously, Schaltenbrand and Putnam (1927) observed that it escaped first from the arteries into the cerebrospinal fluid and a short time later, in smaller concentration, from the veins. In their discussion of the extraventricular sources of cerebrospinal fluid, Schaltenbrand and Bailey (1928) concluded from these results that the vessels of the subarachnoid space must be considered as sources of the fluid.

In studies on vascular permeability in skeletal muscle, Rous, Gilding and Smith (1930) failed to find any vessels larger than fine arterioles and venules permeable to their large series of dyes. Much the same condition with respect to qualitative correlation of vessel size and permeability exists in the skin (Smith and Rous, 1931). As far as is known, though the published data are old and in many ways inadequate (Adamkiewicz, 1882; Kadyi, 1889; Poirier and Charpy, 1892–1902), the vessels of the subarachnoid space are arteries and veins and there are no arterioles, venules or capillaries present. Experience in other regions of the body, therefore, indicates that vessel-permeability in the subarachnoid space is probably insignificant.

Moreover, to conclude from experiments with a single dye that the vessels of the subarachnoid space contribute to the cerebrospinal fluid appears to be dangerous. As pointed out by Rous and his coworkers (1930), comparison of the results gotten with a series of dyes should be made to rule out possible toxic effects of a single dye. Care must also be taken to avoid even slight injury to vessels or changes in temperature or intensity of light, otherwise vessel permeability may be significantly increased (Hudack and McMaster, 1931, 1932). The rate of escape of dyes from vessels can be taken as only a crude index of the normal rate of escape of substances from the blood; in the case of the dyes, escape is much accelerated by a concentration gradient which does not exist for normal substances. The results of Schaltenbrand and Putnam, therefore, are to be considered only suggestive. Final interpretation awaits experience with a large number of substances under carefully controlled experimental conditions. The results which appear most significant in indicating a permeability of the vessels of the subarachnoid space important for the composition and perhaps the quantity of cerebrospinal fluid are those of Cestan and his coworkers.

The data at hand appear to indicate that the amount of fluid arising outside of the ventricles is very small—very much less than that originating within the ventricles. This conclusion is in agreement with the investigations of Riser and Sorel (1928) who attempted to measure, with quite uncertain methods, the amount of cerebrospinal fluid formed within the subarachnoid space. There is a little evidence, far from conclusive, which indicates that small quantities of cerebrospinal fluid may originate from the vessels of the subarachnoid space. It appears more likely, however, that fluid of extra-ventricular origin comes from a sluggish, irregular movement of small amounts of perivascular fluid into the subarachnoid space.

THE ABSORPTION OF THE CEREBROSPINAL FLUID

The Venous Sinuses of the Cranial Dura Mater

In his review of the cerebrospinal fluid Weed (1922) has discussed comprehensively the evidence indicating a major

absorption of cerebrospinal fluid into the large venous sinuses of the cranial dura mater. The background for this view has come from various physiological and anatomical observations. Foreign solutions injected into the subarachnoid space of living animals have been detected in the blood in less than a minute, but appear in the lymphatics only after much time and then in low concentrations. It has consequently been argued that cerebrospinal fluid drains in major part into the venous system. Key and Retzius (1876) and other of the early investigators concluded that passage of fluid from the subarachnoid space into the venous system took place via the Pacchionian granulations of the large cranial dural sinuses. Subsequent research, however, failed to demonstrate these granulations in infants and certain experimental animals, and they were therefore discarded in accepted explanations of the absorption of cerebrospinal fluid.

The problem remained without important contributions until the work of Weed (1914). He examined microscopically the cranial dural sinuses of animals and infants and found in them all so-called arachnoid villi. These villi, in his description, have a cylindrical base of myxomatous tissue lying in a frame-work of fine, reticular connective tissue. The myxomatous basilar structure is capped on all sides by mesothelial arachnoid cells. Many of the villi surround small cerebral veins emptying into the dural sinuses. And, most important, the villi invade the dural walls of the venous sinuses or their lateral lacunae so that the caps of arachnoid cells come in contact with the endothelium of the sinuses. The Pacchionian granulations are considered to be old, hypertrophied villi.

The pathway by which a foreign solution escapes from the subarachnoid space was next studied by Weed with the use of isotonic potassium ferrocyanide and iron ammonium citrate. After irrigating the subarachnoid space with this solution under normal pressure for three or four hours, the animal was killed and promptly fixed with acid formalin. Under these conditions, Prussian Blue granules were precipitated wherever the reagents had been present. Microscopic examination of the material then demonstrated granules of Prussian Blue within the mesothelial cells covering the villi, the endothelial cells lining the venous sinuses and the sinuses themselves. It was consequently concluded by Weed that cerebrospinal fluid escapes from the subarachnoid space into the cranial dural sinuses by way of the arachnoid villi.

This concept is today widely accepted. Halliburton (1916), Cushing (1925), Winkelman and Fay (1930) and many others have adopted it in practically all its particulars. The observations of Le Gros Clark (1920–21) and Winkelman and Fay (1930) on the distribution of the villi and Pacchionian granulations substantiate those of Weed. These structures have been found projecting not only into the sinuses proper but more frequently into the lacunae laterales communicating with the sinuses and formed by terminal arborizations of the cerebral and meningeal veins. Winkelman and Fay at no time found blood in these lacunae and regard them as being filled during life with cerebrospinal fluid. To reiterate, then, cerebrospinal fluid flows from the subarachnoid space through arachnoid villi and Pacchionian granulations into the lateral lacunae and thence into the large sinuses with which these lacunae directly communicate.

Several investigators have expressed doubt that the pathway just described is of importance in the absorption of cerebrospinal fluid. Their criticisms, however,

appear to lack finality. Papilian and Jippa (1925) without valid experimental evidence concluded that this mechanism has no appreciable rôle in the circulation of cerebrospinal fluid. Howe (1929) contended that this explanation is inadequate and that were it correct, fluid must enter the subdural space and subsequently pass through the dura into the venous sinuses. His criticism was apparently made without consideration of the observations showing that the subdural space is obliterated (Weed, 1914; Le Gros Clark, 1920–21) at the point where the villi penetrate the dura and approach its sinuses and that the dura is either a relatively very thin membrane or actually absent over the villi. His suggestion that the villi may be concerned in the entrance of subdural fluid, however, merits investigation.

A new approach to the problem has recently been attempted by Dandy (1929). He reported separation of the brain, with the arachnoid and pia presumably intact, from the longitudinal, circular and transverse sinuses of young dogs. The animals are reported to have been without distress at all times and to have had no evidence of hydrocephalus from four to six months after the operation. Dandy accepts these findings as conclusive evidence that the arachnoid villi are not normally concerned with the absorption of cerebrospinal fluid but that it drains directly into the blood vessels of the subarachnoid space. This conclusion appears doubtful in the light of several objections. Villi have been described by Elman (1923) as being present in the spinal arachnoid membrane. There exist, therefore, mechanisms perhaps like those presumably destroyed by Dandy which may assume the function of the lost villi and prevent abnormally large accumulations of fluid in the cerebrospinal fluid pathways. There appears to be some reason to anticipate this compensation: reduction in the size of the absorbing surface must lead to relatively small increases of cerebrospinal fluid pressure; this pressure-increase causes an increased absorption rate through the intact villi so that accumulations of fluid detectable as hydrocephalus may well be absent. There is a further objection to Dandy's experiments. The statement that all the villi were separated from the sinuses—a difficult operative feat—and the implication that they were without contact with the dural sinuses for six months after the preliminary operation calls for microscopic confirmation. Without this, the possibility of incomplete separation and of villus regeneration, a wholly unexplored problem, cannot be excluded.

It appears justifiable, consequently, to state that the interpretations of Weed are without valid experimental contradiction. The method of determining the normal routes of fluid-flow by means of foreign solutions, the whole basis of the theory, requires, however, most careful and cautious scrutiny before it is to be judged acceptable. Weed himself has been painstaking in his use of the technique. After death, animals were quickly fixed with the precipitating acid-formalin solution. Experiments in which there was diffuse staining of the leptomeninges were discarded as unsatisfactory. There is the possibility, not to be defined quantitatively however, that post-mortem diffusion patterns might have given a picture inaccurate for the living animal. This criticism has its foundation in the thought that the actual time necessary for complete precipitation of the Prussian Blue in the subarachnoid space might have been longer than the apparent time necessary for so-called complete fixation of the tissues. It might be assumed, consequently, that due to a differentiation of the cells of the arachnoid villus, peculiar diffusion

patterns occur within them which lead to the same sort of artifact which long confused the physiology of the kidney. Justification of the method in answer to this criticism is to be found in the failure to detect Prussian Blue granules in the blood vessels traversing the subarachnoid space, in the meningeal vessels, or in the perivascular spaces—the only evident pathways besides the villi from the subarachnoid space to the blood stream. The evidence, therefore, that there exists an important fluid-pathway from the subarachnoid space via the arachnoid villi into the dural sinuses appears extraordinarily strong and merits acceptance of Weed's conclusion that this is an important avenue of escape for cerebrospinal fluid. This conclusion also gains weight from Wegefarth's (1914) demonstration that in the eye the aqueous fluid gains access to the venous sinuses of the sclera through pectinate villi which are analogous in structure to the arachnoid villi. The hesitancy shown by some investigators to accept this explanation and the constant value of confirmatory data urge testing these conclusions with crystalloids other than the Prussian Blue reagents and, if possible, by a totally different method of experimentation.

The Nerve Roots

As has been mentioned, there is reason to believe that a relatively small quantity of cerebrospinal fluid finds its way into the lymphatic system. The pathway from the subarachnoid space has long been identified with the perineural spaces of the spinal and cranial nerves and from them to the lymphatics accompanying the nerves. Both Sabin (1912) and Weed (1914) have failed to find lymphatics in the meninges.

Early investigators, notably Key and Retzius (1876) in their classic studies on the cerebrospinal fluid, concluded that free communications exist between the subarachnoid space and the nerve roots so that cerebrospinal fluid drains directly into the substance of the nerves and the perineural spaces. Later work (see Elman, 1923) has conclusively demonstrated, however, that the subarachnoid space is completely closed, that the arachnoid membrane forms a short cuff about the emerging nerve roots and so isolates the subarachnoid space from any anatomical connection with tissues outside the central nervous system.

Weed (1914) has presented evidence of a functional connection between subarachnoid and perineural spaces. Using his ferrocyanide method for rather long periods and at low pressure, he found granules of Prussian Blue in the perineural spaces of spinal and cranial nerves. His material suggested diffusion of ferrocyanide into lymphatics lying beyond the outer, connective tissue wall of the space rather than direct absorption from the space.

As is implied above, it has been generally accepted that perineural spaces are normal structures accompanying the emerging nerves at least as far as the spinal ganglia. They have been described by Sabin (1912) in human and other embryos and many workers have claimed to have seen them in the adult (see Hassin, 1930b). After dehydrating his material by a special method, Elman (1923), however, found no evidence of them and suggested that they may be artifacts. Nor could he, after irrigating the subarachnoid space with ferrocyanide, demonstrate Prussian Blue granules in the perineural spaces made evident by the usual methods of dehydration.

How, then, if the perineural space be considered an artifact, may foreign solutions and cerebrospinal fluid escape from the spinal subarachnoid space? Elman de-

scribed clusters and columns of arachnoidal cells which invade the spinal dura mater in much the same way as the arachnoid villi described by Weed penetrate the cranial dura. These spinal arachnoid villi were found at the points where the arachnoid membrane was reflected onto the nerve roots and through them Prussian Blue granules could be traced into veins lying outside the meninges. Elman's material permitted no statement about lymphatic absorption. Wislocki and Kubie (1928) found plexuses of small venous sinuses in the spinal dura surrounding the emerging nerve roots. They suggested that the cerebrospinal fluid may drain into these small sinuses of the spinal dura mater via spinal arachnoid villi in just the way that the fluid flows through arachnoid villi into the venous sinuses of the cranial dura mater.

The most comprehensive opinion of absorption around the nerve roots, built on all the available evidence, suggests that small amounts of fluid pass into veins and lymphatics via perineural spaces and spinal arachnoid villi. The pathway in its details, however, is not clearly defined. The only route to the lymphatics for which there is evidence is by way of the perineural spaces and there is some doubt that these spaces are normal structures. There is the possibility, not yet investigated, that fluid may be absorbed by lymphatics lying outside the pachymeninx. It appears probable that small quantities of fluid gain access to the veins in or outside of the spinal dura mater. But again a definitive anatomic pathway has yet to be demonstrated. There are no observations to tell us whether the spinal arachnoid villi are related to veins in the same way as the cranial villi or whether fluid filters through them and then diffuses to neighboring veins either within or without the pachymeninx.

The Blood Vessels of the Subarachnoid Space

It is generally considered that the blood vessels traversing the subarachnoid space are not as small as arterioles and venules and that the leptomeninges are without an intrinsic capillary bed. Doubt exists as to whether or not these vessels receive a covering of mesothelial cells from the leptomeninges. According to Weed (1914) and others, as discussed above, such a covering is invariably present. Schaltenbrand and Bailey (1928), however, were unable to demonstrate such cells either lining the inner surface of the arachnoid membrane or covering the adventitia of the blood vessels. This is a point of importance, for knowledge of the presence or absence of a special cellular layer is fundamental to an understanding of the permeability of the blood vessels of the subarachnoid space.

Dandy and Blackfan (1914) concluded that the absorption of cerebrospinal fluid is a diffuse process taking place directly into the blood vessels of the entire subarachnoid space. They separated spinal from cranial subarachnoid space by ligation of the meninges, injected phenolsulphonphthalein into the spinal space and then recovered the dye from the urine. They reported, however, that absorption from the isolated spinal subarachnoid space was almost as great as from the combined cranial and spinal subarachnoid space. Howe (1929), without adding any valid experimental evidence, concurred in this opinion.

Exception to this view has been taken by Weed (1914 and 1922). He criticized the conclusions of Dandy and Blackfan on the basis of an obviously high cerebrospinal fluid pressure in their phenolsulphonphthalein experiments and possible leakage of the dye into the epidural tissues with direct absorption into the vessels there. He found, moreover, that absorp-

tion from the isolated cranial subarachnoid space was as rapid as from the total subarachnoid space and concluded that the cranial portion of the system contained the essential mechanism, the arachnoid villi, for absorption. These criticisms appear to the writer to lack finality. If dye absorption be accepted as a reliable index of cerebrospinal fluid absorption and possible toxic, diffusion and special absorption effects be neglected, a slightly elevated cerebrospinal fluid pressure such as likely occurred in the experiments of Dandy and Blackfan does not vitiate the demonstration of vessel permeability. Having demonstrated this, the force necessary for fluid exchange in the normal animal can be found in hydrostatic and possibly osmotic pressure differences between the cerebrospinal fluid and venous blood. Nor does it appear reliable to place emphasis on the quantitative disappearance of phenolsulphonphthalein from the subarachnoid space. The factor of error in such experiments has yet to be defined and, as Becht (1920) has contended, dye absorption cannot be taken as a quantitative index of cerebrospinal fluid absorption. Weed's failure to find Prussian Blue granules, after his replacement experiments, in the vessels of the subarachnoid space is not to be taken as conclusive evidence against their permeability to cerebrospinal fluid. It is well known (Stern and others) that the chorioid plexus and ventricular ependyma are impermeable to ferrocyanide though obviously permeable to cerebrospinal fluid; much the same possibility exists in the case of the vessels of the subarachnoid space.

It appears impossible to accept or reject the conclusions of Dandy and Blackfan. The evidence available, however, speaks weakly against a diffuse absorption of cerebrospinal fluid by the veins of the subarachnoid space. The experiments with dye absorption done in an isolated subarachnoid space have been made not only in the presence of the vessels of this space but in the presence of the spinal arachnoid villi. If, as is suggested by the work of Elman and Wislocki and Kubie, these villi are permeable to cerebrospinal fluid and through them fluid passes to the lacunae of the spinal dura, a mechanism is present for understanding the results of Dandy and Blackfan without making their assumptions. The quantitative data at hand are so small and so conflicting that they can fashion no conclusions. The situation is similar to that already found in the discussion of the permeability of the arteries of the subarachnoid space.

The Chorioid Plexus, Ventricular Ependyma and Perivascular Spaces

The conclusion of Askanazy (1914), Hassin (1930b) and others that the chorioid plexus normally absorbs certain constituents of cerebrospinal fluid has been discussed above and found based on experimental evidence of questionable meaning. The chorioid plexus has been implicated, however, in absorption which takes place under abnormal conditions, by investigators who ascribe no such function to it in the normal animal.

When the tonicity of the blood is increased by intravenous injections of hypertonic solutions, cerebrospinal fluid pressure undergoes a precipitous and sustained decrease. This finding has been taken as an indication of increased absorption of cerebrospinal fluid. Investigators have attempted to demonstrate new pathways of absorption caused by the changed osmotic pressure of the blood and, in particular, to probe the possibility that structures generally considered to elaborate the fluid can, under these special conditions, absorb it. Experiments along these lines, therefore, have to do with a decision

as to whether the membranes represented by the vessels, the cells of the chorioid plexus and ventricular ependyma and the structures of the perivascular spaces are permeable to the constituents of the cerebrospinal fluid in one direction only, i.e. from blood to fluid, or in both directions.

Nanagas (1921) injected the Prussian Blue reagents into the ventricles of kittens with experimental internal hydrocephalus and then gave hypertonic saline solutions intravenously. Under these conditions of optimum absorption, he failed to find precipitated Prussian Blue granules in the epithelial cells or vessels of the chorioid plexus. The same lack of evidence for absorption by the chorioid plexus was reported by Wislocki and Putnam (1921) who performed replacement experiments on hydrocephalic animals without using hypertonic solutions. Different results, however, were obtained by Foley (1921, 1923). He followed the Prussian Blue reagents through the chorioid plexus from its epithelial cells into its blood vessels. Forbes, Fremont-Smith and Wolff (1928), in well controlled experiments with Prussian Blue, have recently substantiated the results of Foley.

We are again faced with evidence difficult to evaluate. The work of Forbes, Fremont-Smith and Wolff, however, indicates that under special conditions the Prussian Blue reagents pass from the ventricles through the epithelial cells to the vessels of the chorioid plexus as first found by Foley. This passage of the Prussian Blue reagents through the plexus under the influence of hypertonic solutions is of peculiar interest. As has been mentioned, these reagents fail to pass through the plexus into the cerebrospinal fluid when they are introduced into the blood stream. We are therefore faced with the possibility that either the permeability of the plexus is different in one direction than in another or that hypertonic solutions actually alter the characteristics of the membrane. The last-named possibility appears to be the stronger.

Foley (1921 and 1923) also found evidence of absorption of cerebrospinal fluid by the ventricular ependyma when hypertonic solutions were given intravenously. The same picture was noted by Nanagas (1921) in hydrocephalic animals and he suggested further that this might be an avenue of minimal absorption in normal animals. Much the same results were reported by Wislocki and Putnam (1921) who traced the precipitated granules via the ependymal cells to intercellular and finally perivascular spaces. These experiments probably explain the findings of Dandy and Blackfan (1917). They injected phenolsulphonephthalein into the ventricles of human beings suffering from internal hydrocephalus and found small quantities of the dye appearing in the urine for many days.

Weed (1914) has demonstrated that Mott's (1910) suggestion of a normal pathway of absorption along the perivascular spaces is untenable. He has, however, very strong evidence that hypertonic solutions or experimental cerebral anemia cause a reversal of the normal direction of fluid-flow in the channels and that absorption then occurs. Absorption also takes place apparently directly into the blood vessels of the subarachnoid space after intravenous hypertonic salt.

The weight of evidence consequently appears to support the view that all the membranes identified with formation of cerebrospinal fluid can, under special conditions, absorb cerebrospinal fluid. The case for the perivascular spaces is strong; that for the chorioid plexus and ependyma, weaker. That hypertonic salt causes an important alteration in the character of

all the membranes is suggested by the evidence.

The studies discussed above indicate that normally the largest part of the cerebrospinal fluid is absorbed via the arachnoid villi into the great dural sinuses of the skull. It has been suggested on evidence still weak that fluid also finds its way into the blood stream through the veins of the subarachnoid space and the villi of the spinal arachnoid membrane. A relatively small amount of fluid is thought to drain into the lymphatics from perineural spaces or spinal arachnoid villi. The circulation of the fluid into the veins is presumably maintained by hydrostatic and possibly osmotic forces.

It has been evident throughout this discussion of the absorption of the cerebrospinal fluid that most of the data have come from following the pathways taken by the Prussian Blue reagents under various experimental conditions. Practically all of the present theory on absorption of the cerebrospinal fluid rests on these findings. It is imperative, therefore, that the method of investigation be subjected to as many critical tests as possible. A start in this direction is to be made by following the routes of drainage of crystalloids other than the Prussian Blue reagents from the subarachnoid space into the blood. Until information regarding the passage of other substances from the cerebrospinal fluid into the blood stream is obtained, the present theory of the pathway must remain with inadequate substantiation.

THE CIRCULATION OF THE CEREBROSPINAL FLUID

The generally accepted pathways of circulation of the cerebrospinal fluid have been reviewed by Weed (1922). Briefly, the fluid has been thought to flow from the ventricles into the cisterna magna and from here "slowly seeps downward in the spinal subarachnoid space but passes more rapidly upward about the base of the brain. . . ." The fluid gained by the subarachnoid space in this way receives a relatively very small addition from the perivascular spaces of the central nervous system. In the past ten years some hypotheses and some experimental data have been added to this picture; but, from a quantitative viewpoint, it is still far from complete.

C. v. Monakow (1921) has proposed a pathway of circulation of the cerebrospinal fluid which has provoked considerable discussion. According to him, the ventricular fluid formed by the chorioid plexuses passes through the ventricular ependyma, penetrates into the substance of the hemispheres, and arrives, in part with aid of the neuroglia, in contact with the cerebral parenchyma which it nourishes. The fluid then flows into pericellular spaces and from these via the perivascular spaces into the subarachnoid space. It is consequently possible to distinguish between an afferent fluid from the ventricles to the nerve cells and an efferent fluid from the pericellular spaces through the subarachnoid space to the sites of fluid-absorption (see Stern and Gautier, 1922/23).

This hypothesis has been accepted, among others, by Stern and her coworkers. Stern (1921), Stern and Gautier (1922/23) and Stern and Rapoport (1928) have investigated the passage of foreign solutions from ventricles and subarachnoid space to the tissues of the brain. Excitatory effects have, with few exceptions, been found to be much greater after injection of toxic, foreign solutions into the ventricles than after their injection into the subarachnoid space. In many instances, injection into the subarachnoid space was without detectable effect unless the injection-pressure was high enough to force the foreign substance into the ventricles. This is evi-

dence against the objection that possible escape of the toxic solution into the needle-wound made in the brain by ventricular puncture accounts for the excitatory effects of ventricular injections. Crystalloid dyes introduced into the subarachnoid space failed to stain the nerve tissue. Their introduction into the ventricles, however, produced staining of ependymal, neuroglial and ganglion cells and dye was also found in the pericellular and perivascular spaces and within the arterioles and capillaries, not only of the ventricular wall, but of the cortical surface as well. Similar results have been reported in normal and hydrocephalic animals by Nanagas and Wislocki and Putnam as is noted above. In the view of v. Monakow and Stern these results mean that foreign substances are carried by the cerebrospinal fluid from the ventricles to the cells of the brain; that cerebrospinal fluid circulates from the ventricles into and across the parenchyma of the hemispheres.

This viewpoint has been questioned by Walter (1926) who argued that it is based on incomplete anatomical and physiological evidence and that it cannot be applied to the spinal cord, the central canal of which is without an active circulation of cerebrospinal fluid. Gärtner (1927) remarked that the pressure gradient between fluid in the ventricles and subarachnoid space is probably too small to account for any more than a minimal circulation across the resistance offered by the tissues of the central nervous system. The experiments reported by Stern and her coworkers, by Nanagas (1921) and by Wislocki and Putnam (1921) demonstrate primarily a difference in reaction of the connective tissue elements of the leptomeninges lining the subarachnoid space and of the ventricular ependyma to foreign solutions. This contrast in reaction may be related wholly to inequalities in the toxicity of the foreign substance for connective tissue and ependymal cells, and to differences in diffusion rate of the foreign substance across these cells. It may be without relationship, consequently, to the normal pathway in which the cerebrospinal fluid circulates. The evidence that ependyma has to do with the formation of cerebrospinal fluid is at least as strong as that tending to show that it absorbs and the two functions are difficult to reconcile. The large accumulation of fluid under high pressure which occurs in internal hydrocephalus speaks most forcefully against this viewpoint. Nor is it sufficient, having demonstrated that cells are permeable to the constituents of the cerebrospinal fluid, to conclude that an active circulation occurs across them. Certainly the weight of evidence favors the view that practically all of the cerebrospinal fluid leaving the ventricles gains access to the subarachnoid space without traversing the mass of the central nervous system.

Numerous observations favor the view that there is a definitive current of cerebrospinal fluid flowing from the ventricles through the foramina of Luschka and perhaps the foramen of Magendie into the subarachnoid space. A fair sample of the evidence can perhaps be given by mentioning that Stern and Gautier (1922/23) regularly and rapidly detected substances in the subarachnoid space after their injection into the ventricles. Only rarely, moreover, did substances injected into the subarachnoid space appear in the ventricles and some of these cases are perhaps to be explained by failure to control adequately the fluid-pressure in the subarachnoid space. Schaltenbrand and Putnam (1927), after injecting fluorescine intravenously, observed the dye escaping from the fourth ventricle into the subarachnoid space. It is interesting to note that there was no evidence of fluid-flow through the "for-

amen of Magendie" in cats, dogs or rabbits so that the existence of this communication in these animals has been doubted.

The rate of flow of cerebrospinal fluid from the aqueduct of Sylvius has been measured in etherized cats by Flexner and Winters (1932). In these experiments the fourth ventricle was blocked with a distended rubber balloon. The fluid escaping from the aqueduct was conducted to a bubble-manometer under normal intraventricular pressure by means of a catheter introduced into and through the balloon. It was found that an average of 12 cc. per day of cerebrospinal fluid escaped from the aqueduct. In many animals the rate of flow was highly irregular. Periods of active flow were followed by phases in which no fluid left the aqueduct or in which increase in ventricular volume aspirated fluid from the manometer into the ventricle.

If a correction were made for the cerebrospinal fluid presumably formed by the chorioid plexus of the fourth ventricle, it was found that approximately 0.6 cc. of fluid per hour flowed into the subarachnoid space of the cat. This is obviously a rate of circulation of a very small magnitude. In view of this and the observation that no fluid may leave the aqueduct during certain periods or that fluid may be actually aspirated into the ventricles, it is not surprising that investigators have noted that on occasion dyes introduced into the subarachnoid space have appeared within the ventricles. These factors probably account for the conclusions of Sachs, Wilkins and Sams (1930). These investigators, after studying the diffusion rate of trypan blue in vitro, injected the dye into a lateral ventricle and noted the time necessary for its appearance in the cisterna magna. They concluded that there was no directional current between the ventricles and the subarachnoid space and that the dye spread simply by diffusion.

Many efforts have been made to gain a measure of the rate of circulation in the spinal subarachnoid space. The conclusion of Dandy and Blackfan (1914) that the fluid is removed every four or six hours is based on the rate of absorption of phenolsulphonphthalein. The method has been adequately criticized by Becht (1920): from the results obtained with it nothing can be said of the rate of absorption of the fluid. Sachs, Wilkins and Sams (1930) injected trypan blue into the lumbar subarachnoid space and concluded that the dye spread only by diffusion. Jacobi (1923) concluded there is no true circulation in the spinal subarachnoid space after finding rather constant differences in the protein content of the fluid at various levels of the spinal subarachnoid space. Much the same conclusion was reached by Becher (1921). He believed, however, that there is minimal movement and mixing of the fluid in the spinal subarachnoid space resulting from the rhythmic changes in brain volume which follow cardiac systole and respiration. Recent work (Weed, Flexner and Clark, 1932) indicates that some movement of fluid also follows change in position of the animal; if its position be changed from the horizontal, fluid is dislocated from the uppermost to the dependent portions of the subarachnoid space. Walter (1926), who appears to favor the view that the blood vessels of the subarachnoid space take part in the formation and absorption of the fluid, suggests that in the spinal subarachnoid space formation and absorption of the fluid takes place principally in horizontal planes at places very near to one another. These observations are perhaps representative of the evidence which has led investigators to consider the spinal subarachnoid space without a true circulation.

This conclusion finds substantiation in the observations, mentioned above, on the rate of escape of cerebrospinal fluid

from the aqueduct of Sylvius. There appears to be, in the cat, a definitive movement of fluid from the ventricles to the subarachnoid space. The rate of fluid flow into the cisterna magna is, however, at its maximum extremely small and may, during short intervals, be zero or a negative value due to aspiration of fluid from the subarachnoid space by dilating ventricles. The rate of circulation in the subarachnoid space must in consequence be of a very low magnitude. This accounts for the persistence of differences in chemical constitution of the cerebrospinal fluid at different levels and for the importance of diffusion in the spread of foreign substances injected into the fluid. More exact statements await the determination of the volume of the subarachnoid space, a quantity which has yet to be well measured. It is perhaps fair to add, however, that due to its greater absorbing surface, more fluid passes through the cranial than through the spinal subarachnoid space.

THE BARRIER BETWEEN BLOOD AND CEREBROSPINAL FLUID

It is well known that many foreign substances introduced into the blood stream do not escape into the cerebrospinal fluid or central nervous system. To the mechanism responsible for this protection of the nervous system, Ehrlich gave the name of barrier. Subsequent thought attempted a more specific designation with the result that passage of substances from blood to cerebrospinal fluid was identified with the permeability of the leptomeninges. Failure of a substance to pass from blood to fluid or nervous system was attributed to impermeability of the meninges and the whole subject was, and often is still today, considered under the title of meningeal permeability.

Among others, Stern (1923) has objected to the use of this term. Although admitting the impossibility of identifying precisely the anatomical substratum of the barrier, she concluded that neuroglia, ependyma, chorioid plexus and vascular endothelium all were likely involved in addition to the meninges and she proposed the term "Barrière Hémato-encéphalique." Walter (1929) is one of many of the German school who, like Stern, prefers to retain the inclusiveness of Ehrlich's term and writes of the "Blut-Liquorschranke." Zylberlast-Zand (1924), however, concluded that the term meningeal permeability is exact in its implications. Justification of any particular designation quite obviously must come from consideration of anatomical and physiological studies having to do with the nature of the membranes between the blood and the central nervous system.

The approach of choice to the physicochemical nature of membranes placed between the arterial blood and central nervous system involves a comparative study of the chemistry of blood and cerebrospinal fluid. This is a long and complex subject, however, and will be discussed elsewhere (Flexner, 1934). We shall consider here briefly experimental data concerning the passage of a few foreign substances from blood to fluid and the evidence available on the anatomical substratum of the barrier.

Stern and her coworkers (Stern, 1921; Stern and Gautier, 1921–22; Stern and Rapoport, 1927a) have published many experimental data on the passage of substances from blood to cerebrospinal fluid and nervous system. It has been their object, in part, to determine whether the physical properties of size and charge of particles introduced into the blood account for their behavior at the barrier. This has been tested most simply by comparing results obtained with groups of substances, each group being composed of members with certain physical properties of assumed equivalence. Stern has concluded

that no chemical law offers an explanation of the function of the barrier. Anions such as bromide and chloride pass into the cerebrospinal fluid from the blood with ease; iodide, though highly diffusible, is to be found in the fluid only in very small amounts even though its blood concentration be high.

Using a large series of dyes and inorganic compounds, Wittgenstein and Krebs (1926) came to the conclusion that all anions pass the barrier from blood to cerebrospinal fluid. Their series included ferrocyanide and Orange G, with which Stern and others have had negative results. Basic dyes, however, were not to be found in the cerebrospinal fluid, nor did colloidal dyes pass the barrier. The results of Wittgenstein and Krebs show complete uniformity in the behavior of a particular group of substances. Ions having a positive charge are adsorbed by the negatively charged proteins of the plasma and are not available for passage across the barrier. Negatively charged ions, free in the blood plasma, pass the barrier. Colloids, because of their size, fail to go into the cerebrospinal fluid. These results find disagreement not only in the findings of Stern but also in the work of Wesselkin (1930). Wesselkin found that certain acid dyes failed to pass the barrier whereas basic dyes stained the central nervous system.

These results are sufficient to indicate that very little is known of the exact behavior of the barrier to foreign substances in the blood. Nor is this surprising. The method of investigation lacks refinement. Too little account has been taken of the dosage of foreign substances injected into the blood and of the maximal limit of concentration beyond which toxic effects produce an abnormal barrier. No effort has been made to test the permeability of the barrier in these experiments and to prove it unaltered for normal or abnormal constituents of the blood. Nor has the state of these foreign substances in the plasma been determined. Each and all of these factors must be known before the function of the barrier can be understood and an almost complete lack of understanding at the moment makes futile an attempt to evaluate the available data.

It is of interest to note at this point that all crystalloids placed in the subarachnoid space quickly appear in the blood stream. Ferrocyanide, not detected by most investigators in the cerebrospinal fluid when present in the blood, rapidly passes from the fluid into the blood. The membranes placed between the arterial blood and the central nervous system are quite clearly different than those separating the cerebrospinal fluid and the venous blood. In the understanding of the behavior of these membranes lies the understanding of the mechanism by which the central nervous system is protected from noxious substances and by which it rids itself of such substances—a subject of fundamental importance in the physiology, pathology and therapeutics of the central nervous system.

Three principal concepts have been advanced as to the anatomical substratum of the barrier. It is clear that variation of opinion must come in part at least from the several divergent views of the origin of the cerebrospinal fluid. Wherever fluid is formed, membranes must be placed between it and the blood; the tissues of the barrier will be more numerous, the greater the number of assumed sites of fluid-formation. The simplest concept considers the epithelium of the chorioid plexus identical with the barrier. The old theory of a true meningeal permeability also has its adherents. The most comprehensive view involves the functional synergy of many tissue elements including the epithelium of the chorioid plexuses, the ependyma of the ventricles, the endo-

thelium of the cerebral capillaries and the neuroglia placed between the blood vessels and the nerve cells.

Mestrezat (1912) considered the chorioid plexuses alone to regulate the composition of the cerebrospinal fluid. This view has been substantiated by observations first made by Goldmann (1913), in which trypan blue was found in the epithelial cells of the plexus and the adventitial cells of the blood vessels after intravenous injection, though it was missing in the cerebrospinal fluid. When the dye was placed directly into the ventricles, however, Goldmann found that it passed through the ependyma to underlying cells, indicating that the ependyma is not a barrier to its passage as are the epithelial cells of the plexus. These observations of Goldmann have been frequently confirmed (see Gärtner, 1927) and have led to rather wide acceptance of the view that the chorioid plexus is a selective filter through which certain substances cannot pass from blood to central nervous system.

The work of Zylberlast-Zand (1924) has directed attention anew to a true meningeal permeability. This author, like other investigators, has identified histiocytes in all the connective tissue elements of the central nervous system and it is her theory that these histiocytes constitute the barrier between blood and cerebrospinal fluid. The theory has as one of its important foundations an experiment carried out on several kinds of animals. Trypan blue, given intravenously, failed to stain the nervous tissue of the normal animal. If, however, the superficial pia mater was destroyed by scarification or freezing, the brain beneath it became stained. Hence, presumably, a demonstration of the protective rôle of the pia mater and its histiocytes. In such experiments, however, the pia mater in all probability is not changed alone; the walls of the blood vessels of the area are likely damaged and their permeability greatly altered. The experimental basis for the theory is consequently inadequate. The hypothesis for this reason and because of several untenable implications cannot be considered acceptable. It has its value, however, in directing attention to the histiocytes of the mesodermal tissues of the central nervous system as a possibly important part of the anatomical substratum of the barrier.

Cestan, Laborde and Riser (1925) injected foreign substances into the blood and a short time later found them in practically equivalent concentrations in fluid from the lumbar subarachnoid space and the cisterna magna. They appreciated the dangers of artifacts and attempted their elimination. The conclusion drawn from these results is that the blood vessels throughout the subarachnoid space and central nervous system in addition to the chorioid plexuses, regulate the passage of substances from the blood. Meningeal permeability, according to these authors, merits its name though fundamentally it is to be regarded simply as a vascular permeability. These results are so far reaching in their implications that they call for confirmation.

The first element in the barrier was considered by Gärtner (1927) to be the walls of the blood vessels. Substances having passed the vessels encountered either the most important part of the barrier, the epithelial edge of the chorioid plexus, or the largest part of the barrier, the membrana limitans gliae. This glial "membrane," placed between the nervous tissue and the connective tissue of its blood vessels, was considered by Gärtner to be present in practically all regions of the brain between ectoderm and mesoderm. Its relationship to the barrier was first indicated by the escape of trypan blue

where it was lacking; for example, from the blood vessels into the ectodermal tissue of the posterior lobe of the hypophysis, and the complete protection of tissues when it was present. Puncture wounds of the brain were made and at various periods thereafter trypan blue was given intravenously. Much staining of the mesodermal-glial granulation tissue always followed; staining of the ectodermal tissue was never noted. The glial membrane, therefore, in Gärtner's view is a part of the barrier to passage of colloids from the blood. It is to be regarded not only as a boundary between mesoderm and ectoderm but also between the colloid-containing blood plasma and the colloid-free cerebrospinal fluid.

A very comprehensive view of the tissue elements composing the barrier has been advanced by Stern and her coworkers (see Stern, 1929). In it, as has been mentioned, are included all the cells which form the boundary between mesoderm and ectoderm; the epithelium of the chorioid plexuses, the ependyma of the ventricles, the walls of the cerebral blood vessels, the neuroglia.

It was noted by Stern and Rapoport (1927b) and by Stern and other of her collaborators (see Stern, 1929) that experimental alterations in the character of the barrier might affect its permeability for colloids without affecting its permeability for crystalloids or, conversely, an alteration in crystalloid-permeability might occur without change in colloid-permeability. Thus in the newly born animal, unlike the adult, the crystalloid, ferrocyanide, passed the barrier whereas trypan blue failed to enter the central nervous system. In cases of experimental carbon monoxide poisoning or thyroidectomy, permeability for crystalloids remained unchanged while permeability for colloids increased. After increasing the osmotic pressure or pH of the blood, there was evidence of an increase in permeability for all types of substance. Findings of this sort led to the interesting speculation that two different sets of anatomical elements governed the permeability to crystalloids and colloids.

There followed an attempt to verify this hypothesis histologically. The histological picture after escape of a foreign crystalloid into the central nervous system was entirely different than after escape of a colloid. Ferrocyanide, having escaped into the cerebrospinal fluid, was to be identified as Prussian Blue granules principally within the epithelial cells of the chorioid plexuses which usually showed pathological changes. Prussian Blue was also to be seen in the walls of the ventricles, but never in the walls of the blood vessels of the central nervous system. Trypan blue, on the other hand, having escaped into the cerebrospinal fluid, was to be found in the walls of the blood vessels and in the perivascular spaces. The findings suggested that the passage of trypan blue was to be related to alterations in the permeability of the blood vessel walls whereas ferrocyanide entered the central nervous system because of a change in the permeability of chorioid plexus and ependyma. The regulation of the passage of crystalloids into the cerebrospinal fluid was consequently attributed in large part to the chorioid plexus; the regulation of the passage of colloids, to the cells of the vessel walls.

The investigation of the anatomical substratum of the barrier has produced contradictory opinions as have the studies of its function. There is evidence that entering into its formation are histiocytes, glia, ependyma, the epithelium of the chorioid plexuses and the tissues of the blood vessels. Nor is this surprising. All these cells have been known to ob-

struct the passage of colloidal dyes across them. The situation loses its clarity, however, when we question the quantitative part played by each of the constituents. Most investigators stress the importance of the epithelium of the chorioid plexuses—and this is in agreement with our present theories of fluid-formation. Others, however, point to the histiocytes, glia or blood vessels as furnishing the important membranes. It is well to leave this a problem open for future work to be guided but not too much influenced by the work of the past. So too with the problem raised by Stern—the possible difference in the morphological basis for impermeability to certain crystalloids and to colloids.

THE FUNCTIONS AND SIGNIFICANCE OF THE CEREBROSPINAL FLUID

The cerebrospinal fluid has long been regarded as affording protection to the central nervous system. It helps to support the weight of the brain, tends to distribute equally the force of blows, serves as a lubricant between the bony axis and the brain and spinal cord (Aycock, 1925). In addition to these rather obvious purposes, it has another important mechanical function. The skull and vertebral column have a capacity which is practically constant and both are completely filled with central nervous system, blood and cerebrospinal fluid. Variation in the volume of any one of these constituents must be met by reciprocal compensation in the volumes of the others. The cerebrospinal fluid, therefore, through alterations in its quantity, permits changes in the volume of the central nervous system and the vascular bed within the bony axis (Flexner, Clark and Weed, 1932). Because changes in its volume probably occur relatively slowly, it serves to protect the central nervous system from sudden changes in the amount of blood coming to it.

A problem of major interest revolves about the relation of the cerebrospinal fluid to the metabolism of the nerve cells. Many authors have considered it to bring nourishment to the nerve cells and to carry their metabolites away. Such a view, for example, is the inevitable consequence of von Monakow's schema of the intracerebral circulation of the fluid discussed above. To present here the various contradictory opinions which have grown up about this point would simply involve a reëxamination of the anatomical and physiological data already presented. We shall consider, therefore, only that point of view which appears to fit best the acceptable experimental findings.

All the organs of the body, excepting the central nervous system, have lymphatics. It is a function of these vessels to drain away that part of the tissue fluid with its metabolites not returned directly to the blood. The lymphatics are consequently a most important link in the regulation of fluid distribution. The perivascular spaces appear to fill this need within the brain and spinal cord. Fluid leaves the capillaries of the central nervous system to nourish its cells, and that part, with its products of metabolism, not returned directly to the blood, flows through the perivascular spaces to the subarachnoid space.

The larger quantity of cerebrospinal fluid coming from the ventricles can nourish only those cells which border upon its pathway of circulation—the ependyma of the ventricles, the cells of the leptomeninges and possibly, in an incomplete way, a thin layer of cells lying below those named. The ventricular fluid probably performs the more important function of washing into the venous system the products of tissue metabolism which are

discharged into the subarachnoid space from the perivascular spaces.

It is perhaps worth while to conclude this review by pointing out that the cerebrospinal fluid presents problems of physiological and clinical interest not fully considered here. It must be given a major part in all comprehensive discussions of intracranial pressure and intracranial circulation. An understanding of the chemistry of the fluid and its mode of separation from the blood is necessary to the better understanding of the membranes of the body and to the problem of fluid distribution within the body. In this connection and in others, it must be emphasized that practically all that is known of the fluid has come from studies on mammals. There are but few investigations on submammalian forms from which much might be contributed to a better understanding of all of its problems.

Beyond the clinical interest of disorders such as hydrocephalus, knowledge of the rate and pathways of circulation, of the absorption and mode of origin of the fluid is needed for intelligent therapeutic measures within the central nervous system. For though the brain is guarded by the absence of a true lymphatic system continuous with that of the rest of the body and by special membranes placed about its vessels, it is, because of this protection, inaccessible to many of our weapons against disease carried to other organs by the blood.

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THE CHANGING CONCEPT OF OVARIAN RHYTHMS

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THE day is not in the far distant past when schools, medical as well as others, alike taught their students that all germ cells in the mammalian ovary were irrevocably formed during foetal life, and thereafter grew to maturity at stated times during adult life. Curiously enough, this static condition in the germ cells and germinal epithelium was not considered incompatible with what was recognized as regular rhythms in ovarian functional activities other than the production of germ cells. These were the regularly recurring oestrous periods in the lower mammals and menstrual cycles in the primates, with the maturation of follicles, ovulation, and the formation of corpora lutea. In other organs of the body also it was granted that the cells were constantly breaking down and being replaced by newly-forming ones, from which arose the popular idea that the body was renewed every seven years. Why the germ cells should be an exception so strikingly unlike other tissues of the body no one has attempted to explain.

When the amount of work that has been done on the mammalian ovary in the past twenty years is considered, it is truly remarkable that the actual facts concerning the production of germ cells should have received so little recognition among biologists. Yet it is a question of great biological as well as practical importance.

THE EVIDENCE FOR PERIODIC FORMATION OF GERM CELLS THROUGH ADULT LIFE

The modern attack on this problem may be said to have begun with the work of Arai in 1920, though he was not the first to suggest that there was a continuous formation of germ cells through adult life. Before this period there were many references to such a possibility, a tabular summary of which is given in table 1. These observations were made on a wide variety of mammals, including man, and indicate a striking uniformity in results. It is generally conceded that Pflüger (1863) was the first to describe the ingrowths of new cells from the germinal epithelium, the classical Pflüger's tubes, but he also believed that this new growth was periodic, recurring at each mating season. During the same year Schrön noted an increase in the number of young ova immediately beneath the germinal epithelium in cats and rabbits during oestrum and in the human during menstruation. This idea of a periodic production of new germ cells brought out by these investigators, lay in fallow ground until the work of Allen appeared in 1923, when he described a cyclical production of new germ cells during each oestrous cycle in the mouse.

In the earlier work the next important contribution was that of Paladino (1887, 1888, 1903). He studied a wide range of animals and concluded that there was a continual degeneration of both ova and follicles and continuous regeneration of these from the germinal epithelium throughout adult life. As we shall see later, these two conclusions, a degeneration and regeneration of ova and follicles from the germinal epithelium, with a periodic reformation of these, discovered by these early investigators, cover the essential facts brought out by the latest

TABLE 1

Tabular Summary of Literature on New Germ Cells Produced in Adult Life in Mammals

MAMMAL	AUTHOR	REMARKS
Bat	Van Beneden (1880)	Ova in germinal epithelium
Mouse	Harz (1883)	Ova in germinal epithelium
	Lange (1896)	Ova in germinal epithelium
	Allen (1923)	Ova in germinal epithelium
	Brambell (1927)	Ova produced rhythmically
Rat	Arai (1920)	For at least one year after birth
	Butcher (1927)	Ova from germinal epithelium
	Swezy (1929)	Continuous production of ova
	Hargitt (1930)	Continuous production of ova
	Evans and Swezy (1931b)	Rhythmical production of ova
Guinea pig	Harz (1883)	Ova in germinal epithelium
	Paladino (1888)	Continuous production of ova
	Papanicalaou (1924)	Continuous with varying intensity
	Evans and Swezy (1931b)	Rhythmical production of ova
Rabbit	Schrön (1863)	Increase in new ova at oestrum
	Coert (1898)	Ova in germinal epithelium
	Lane-Claypon (1905)	From interstitial cells
Ferret	Robinson (1918)	Development from germinal epithelium
Cat	Pflüger (1863)	Periodical ova from epithelial tubes
	Schrön (1863)	Increase in new ova at oestrum
	Harz (1883)	Ova in germinal epithelium
	Coert (1898)	Ova in germinal epithelium
	Evans and Swezy (1931b)	Rhythmical production of ova
Dog	Waldeyer (1870)	Cords from germinal epithelium
	Wagener (1879)	Epithelial thickenings
	Paladino (1888)	Continuous production of ova
	Evans and Swezy (1931b)	Rhythmical production of ova
Cow Bear Pig Goat Horse Dolphin	Paladino (1888)	Continuous regeneration of ovary from germinal epithelium through adult life
Lemur	Rao (1927)	Epithelial cords and cells
Monkey	Evans and Swezy (1931b)	Rhythmical production of ova
Man	Schrön (1863)	Increase in new ova at menstruation
	Koster (1868)	Epithelial ingrowths
	Amann (1899)	Ova in germinal epithelium
	Paladino (1888)	Continual formation
	Fellner (1909)	Epithelial cords and single cells
	Evans and Swezy (1931b)	Rhythmical production of ova

studies on this material, though they have hitherto received but little recognition from biologists generally.

Other contributions through this period were fragmentary, though confirming the work already noted, describing the appearance of ova in the germinal epithelium and the ingrowth of epithelial cords from the germinal epithelium. With the work of Arai in 1920 a new attack on the problem was made. He counted the number of ova and follicles in the entire ovary of a number of rats at all ages and decided that ovogenesis was a continuous process. This was followed by the similar studies of Allen in 1923. His systematic study of a series of ovaries of mice through the entire oestrous cycle confirmed the conclusions of Pflüger and Schrön that there was a periodic formation of new germ cells. He found that mitoses in the germinal epithelium, which he considered preliminary to germ cell formation, were more numerous at oestrum than at other periods of the cycle, with an average of 400 to 500 new ova being formed in each oestrous cycle. This was followed by degeneration, only about one per cent of them surviving. Later (Allen, Kountz, and Francis, 1925), he found that the greater part of this degeneration took place among the follicles, where the ratio of degeneration was about 85 per cent.

These results were confirmed by Papanicalaou (1924) on the guinea pig, though he considered ovogenesis a continuous process which varied in intensity, being modified by seasonal conditions, but especially by an active corpus luteum. He concluded that follicles must grow or die; it was impossible for them to persist for any length of time. Like Allen, he found that only a few follicles survived to maturity.

Butcher (1927) studied the immature and adult rat, finding that ovogenesis was a continuous process but adding no new information as to its periodicity. This was further confirmed by Swezy (1929) and Hargitt (1930). The latter author discussed the probability of a periodic formation of new germ cells but was inclined to believe this was a continuous process in this animal.

The studies of Evans and Swezy (1931b) extended the work of these investigators both intensively and extensively. It was shown that ovogenesis occurred throughout adult life in the rat, guinea pig, dog, cat, monkey, and man, by outgrowths from the germinal epithelium, either as single cells or as epithelial cords. It was also shown that this production of new germ cells was a rhythmical process, closely related to the ovarian rhythms characterized by maturation of the follicles, ovulation, and the formation of the corpora lutea. During the middle of the ovulation or ovarian cycle, metoestrum and anoestrum in the lower mammals, there was an extensive proliferation of new germ cells from the germinal epithelium, with the growth of many small and medium sized follicles, along with regression of the corpora. Towards the end of the cycle, at the time of ovulation, there was a drop in the production of new germ cells and a slowing up of follicular growth, with atresia of all follicles which did not ovulate. The beginning of the new cycle was marked, a short time after ovulation had occurred, by a resumption of growth, both in the production of new ova from the germinal epithelium and in the growth of small and medium sized follicles. These alternate phases of growth and regression take place in each ovarian cycle. The dictum of Papanicalaou that all follicles must grow or die was extended by showing that the germ cells, far from being long lived, probably have the shortest life span of any group of cells in the body.

Animals with a short cycle, as the rat and mouse, form the most unfavorable material for these investigations, since the length of time necessary for complete growth of follicles, as well as complete atresia, is so near the entire length of the oestrous cycle that these relations are obscured. The guinea pig, with its cycle of about sixteen days, is one of the best for this purpose, the ovary showing clear cut pictures for each phase of the cycle.

It is thus seen that a fairly large number of mammals have been recorded as showing evidences of the cyclical formation of ova and follicles throughout adult life. In a still greater number it has been shown that ovogenesis occurs during adult life, the lack of serial study of ovaries of many individuals obscuring the periodic relationships. The wide variety of animals which have been used strongly suggests that these conclusions are applicable to the Mammalia generally.

EVIDENCE AGAINST PERIODIC FORMATION OF GERM CELLS

An equally large number of investigators, working on the same animals, found no evidences of such new formations of germ cells during adult life, though large cells in the germinal epithelium were noted in most cases. One stumbling block to the recognition of these cells as germ cells has been the lack of maturation phases in the formation of chromosomes, as reported by Cowperthwaite (1925), and others. It has been definitely shown by Kingery (1917), Allen (1923), Brambell (1927), Swezy (1929), Hargitt (1930), and Evans and Swezy (1931b) that such phases do not occur in the definitive ova in mammals which have been carefully investigated.

Others, as Kingsbury (1913), felt that an attempt to explain the presence of these cells was unnecessary, and Waldeyer, though finding new germ cells in adult dogs in his earlier studies (1870), in his later paper (1906) states his belief that ovogenesis does not occur in the adult, though admitting a prejudice by saying that the establishment of this concept would controvert Weissmann's theory, which he believed.

PROLIFERATION AND DEGENERATION OF OVARIAN TISSUES

The components of the ovary may be divided into two main divisions, the fundamental structures and the generative portion, the former composed of stroma, connective tissue, blood vessels, etc., and the latter of germinal epithelium, tunica albuginea, germ cells, interstitial cells, follicles, and corpora. The rhythms of ovarian functioning are participated in, to some extent, by the first group, but it is the generative portion of the ovary which produces the striking changes noted at oestrum and anoestrum. In the formation of follicles and corpora the connective tissue and blood vessels play a part, these tissues thus having a proliferative phase, followed by a degeneration of the new tissue thus formed, coextensive with the phases of growth and regression of the follicles and corpora. In the generative portion the amount of new germ cell and follicular tissue thus formed in each cycle is enormous and an equal amount of degeneration takes place in each cycle. This may readily be seen by comparing the pictures presented by the ovary at anoestrum with that at oestrum, particularly in the dog and guinea pig (Evans and Swezy, 1931b). These ovarian rhythms are not confined to the maturation of follicles, ovulation, and corpora formation, as was commonly supposed, but include a proliferation of new germ cells, and furthermore, extend to the fundamental structures of the ovary itself, periodical growth, followed by degenera-

tion and absorption of the tissues thus formed, being found throughout the entire organ. As was first pointed out by Paladino (1888), the germinal epithelium is the important factor in this periodic regeneration of these ovarian structures, from it arising ova, follicles, corpora lutea, and interstitial cells. It is thus the fundamental basis from which arise all ovarian changes.

THE RELATION OF OESTRUS AND MENSTRUATION TO OVULATION

The regular recurrence of oestrous periods in the lower mammals and menstruation in the primates has long been a matter of common knowledge, but it remained for investigators in recent years to show that these external manifestations were connected with an equally regular recurrence of certain events in the ovary. A review of the literature on this question is outside of the scope of this paper, an ample discussion of the earlier work being found in Marshall (1922). In those of the lower mammals which have regular cycles, it has been found that ovulation takes place at a time which can be predicted in a fairly definite manner (Stockard and Papanicalaou, 1917; Long and Evans, 1922). This fact has become the basis of most of the experimental work on the interrelations between the gonads and their controlling hormones. So close is this relation between the oestrous cycles and the ovarian cycles in these animals that the period of the oestrous cycle can be determined with a high degree of accuracy by an examination of the ovary. This is important in that it indicates that the length of each phase of the ovary is fairly stable in a given species or strain, under normal conditions, with an adequate food supply. Thus, in the guinea pig (Loeb, 1911; Evans and Swezy, 1931b), the tenth to the twelfth days of the oestrous cycle will invariably show the presence of many follicles in the ovary, with the first evidences of regression in the corpora lutea, while prooestrum will show much follicular atresia, along with a few maturing follicles. Anoestrum in the opossum (Hartman, 1923) is always accompanied by the presence of great numbers of follicles, most of which are atretic. In the pig (Allen, Kountz, and Francis, 1923), macroscopic examination is sufficient to determine the approximate period of the oestrous cycle, follicles of three to six millimeters in size not being present before about the eleventh day and larger than these from about the fifteenth day, with a complete disappearance of all visible follicles after ovulation. The work of Allen, Pratt, Newell, and Bland (1930) on the human ovary shows the same periodicity. In their descriptions of 35 ovaries, they show that follicles less than seven millimeters were present in four, follicles between seven and ten millimeters in seventeen, and fourteen contained follicles larger than ten millimeters, this size being considered an ovulation size. Comparing these data with those given for the pig and the lower mammals, it is evident that the first group, with only small follicles, was near the beginning of the ovarian cycle, the second group, with follicles from medium up to ovulation size, was at the middle up to the preovulation period, and the third group at the ovulation period. The total lack of any recognizable relation between these ovarian phases and the periods of the menstrual cycle at which they were found agrees with the conclusions noted below. The ovaries with only small follicles were found at days twelve, sixteen, seventeen, and twenty-two, those with follicles of ovulation size occurred at days two, eight, nine, and up to twenty-three, and medium sized follicles at all dates from the second to the twenty-third.

Long continued observation of single individuals by a number of investigators produces evidences that, while the length of the oestrous cycle may vary from individual to individual of a species or race or even a particular strain, yet it tends to be fairly regular in a single individual, each seeming to have its own special rhythm. There is some evidence that these cycles have less tendency to great variation in larger animals than in the smaller ones, such as the rat and mouse, under laboratory conditions. This seems to apply equally well to the ovarian phases which accompany these cycles.

In animals like the cat, where there is no necessary correspondence between the ovarian phases and the oestrous cycles (Evans and Swezy, 1931b), this lack seems to be only in the oestrous cycles, which are irregular, varying from a few days to two months or more in length, while the ovarian cycle exhibits the same regularity noted in other animals, with a periodicity of about seventy-five days. In the primates also there is no exact correspondence between the ovarian cycles and the menstrual cycles (shown in the data given by Schröder, 1930, though not in his conclusions, and in the work of Allen *et al.*, cited above, among others), though each seems to have the same periodicity of about twenty-eight days. Even with this lack of synchronism, however, all the evidence points to a regular rhythm in their occurrence, a rhythm which seems to be as fundamental in the primates as in the lower mammals, with the same manifestations of alternate growth and regression in all of the components of the ovary, with its associated growth and regression in the uterus. This rhythm, as we will show, is dependent on the reactions between certain hormones (Moore and Price, 1932; Evans and Swezy, 1933), and, since these hormones are alike in all mammals, it is to be expected that the functional changes resulting from them would be similar.

Considerable discussion has taken place around the question of the relation of the ovulation cycle to the menstrual cycle, and the statement made above is by no means generally accepted; yet, when all the facts are considered in connection with this fundamental importance of regular rhythms in both morphology and physiology in the ovary, with the data given by many investigators, including the dissenters, no other conclusion seems tenable. It has been shown (Evans and Swezy, 1931a) that the available data, gathered from many sources, clearly indicate that ovulation may take place at any time in the menstrual cycle, though tending to occur more frequently during the middle third of the cycle. Some investigators maintain that it can occur only at the mid-interval period, though Allen *et al.* have shown that follicles of ovulation size may be found at all periods ranging from day two to twenty-three, as noted above.

It was first shown by Sutton (1886) that menstruation may occur without corpora in the ovary of the monkey, with a low interval type of uterus. Other early investigators (De Sinety, 1881; Heape, 1897; Möriche, 1882; Lipes, 1904; Oliver, 1906, 1907) had indicated the same thing. This was fully confirmed by the later work of Corner (1927), Allen (1926), and Hartman (1927). This fact, so contrary to the generally accepted view, in itself is good proof that menstruation is independent of both ovulation and corpora formation, and hence seems to invalidate the idea of a close relation between the two cycles, and particularly the idea that the regression of the corpus is related to the appearance of the following menstrual period. The latter assumption seems to rest mainly on theoretical grounds, all of which are contradicted by the evidence

just cited. There are no exact data indicating how long the corpus is functional but the consensus of opinion seems to be that it is about ten days. Since ovulation occurs more frequently during the middle third of the cycle, this results in the more frequent appearance of regressing corpora near the time of menstruation than corpora in other phases. There is evidence that they occur at other times also.

In investigating the relation between ovulation and the menstrual cycle, the greatest emphasis has been placed on the finding of tubal eggs, both in the human and in the monkey. The dates on which these have been reported range from the tenth to the nineteenth day of the menstrual cycle. In his most recent summary of work on the monkey, Hartman (1932) reports "111 accurately determined ovulation days," his data being derived from gynecological evidence, time of conception, and ovulation as determined by palpation. These days range from the ninth to the twentieth day of the menstrual cycle. In an earlier paper Hartman (1929) concludes that the midinterval bleeding in primates occurs as a result of the congestion following ovulation. The range of time during which this has appeared in his monkeys he gives as the seventh to the eighteenth day. Adding these to the list given above, the range of time during which ovulation has apparently occurred in these primates extends from the seventh to the twentieth day of a twenty-eight day cycle. It must be further noted that more animals have been examined during the middle of the cycle than at other periods. The range of variation shown in these results is so great that it is at once evident that we must discard the idea that ovarian function is fundamentally rhythmical, or else discard the idea that there is a fixed relation between the ovarian and the menstrual cycles. It may be questioned whether the average or mean time has any value in judging this relationship. If the two cycles are definitely related the variation in the one should correspond to the variation in the other and this is not the case, as may be seen in Schröder's tabulation.

The menstrual cycle is remarkable in its regularity. In the cases under discussion the cycles were regular in some instances. If we consider the regression of the corpora related to the following menstruation, we must believe that the corpora in these cases had a functional life span varying from eight to twenty-one days. Our knowledge of the regularity of the menstrual cycle and the regularity of the oestrous and ovarian cycles in the lower mammals at once leads us to cast out this as a working hypothesis. It seems fairly certain that the corpora formed at day nine will regress in approximately the same time as those formed at day twenty, in which case the menstrual period will show corpora in advanced stages of regression. That the menstrual period does coincide with all stages of regression and growth of the corpora is amply proven by Schröder's (1930) careful examination of portions of uteri from 898 human cases, the uterus being an accurate criterion of the phase of development of the corpus. So far as the facts go, there is no evidence that the ovarian cycle in the primates is more erratic than is the menstrual cycle, or the cycles of the lower mammals, a theory we must accept if we consider the two cycles as having a necessary time relation. All the evidence in the lower mammals indicates that these periods are relatively stable in most species. Neither is there any valid evidence that these processes are radically different in the primates from those prevalent in the lower mammals. This is true in the morphology of the ovary (Evans

and Swezy, 1931b), as well as in the results obtained by the response of monkeys to the experimental administration of hormones (Hartman and Squier, 1931; Smith and Engle, 1932; and others).

Closely paralleling these changes in the ovary, it has been shown that the uterus also functions in cycles as regular as those of the ovary, its period of greatest development coinciding with the ovulation period and the functional life of the corpus, and its regression with the first beginnings of regression in the corpus. This has been most convincingly demonstrated by Schröder (1928) in the human, Loeb (1911) and Stockard and Papanicalaou (1917) in the guinea pig, Corner (1921) in the sow, Long and Evans (1922) in the rat, among others. In the earlier work that of Heape (1900) stands as an important landmark. In addition to these morphological contributions, much experimental work by many investigators proves, beyond a doubt, that these uterine cycles are intimately bound up with the ovarian cycles of follicular growth and maturation and corpus formation and regression, the hormone secreted by the follicles causing early growth and the progestin from the corpora continuing its fullest development. So close is this relation that, as we have pointed out in an earlier paper (Evans and Swezy, 1931a), a study of the uterus gives more reliable information concerning the phase of the ovarian cycle than does a study of the ovary itself. This is especially true of the corpora, since regression in the uterus will be evident before the corpus shows marked indications of it, the change in hormone production being a more delicate test than morphological changes and seeming to occur earlier. In animals where ovulation may not occur without copulation, as in the cat, the only reliable test of the presence of the ovulation period is found in the degree of development of the uterus, a certain amount of growth always occurring before ovulation. When the mature follicles degenerate without ovulation, immediate regression of this new growth takes place in the uterus (Evans and Swezy, 1931a), with an earlier reversion to the low interval type of structure than is found when a corpus is present. Definite cycles occur with or without an accompanying ovulation, the amount of growth attained by the uterus and the length of time after the ovulation period before it begins to regress, being the only apparent differences between them.

In the great amount of experimental work that has been done (Leonard *et al.* 1932, and others), showing that the folliculin present near the end of the growth phase in the ovary is the stimulus for the development of the uterus, followed by other definite changes with the production of progestin by the corpus, ample evidence is given that these morphological changes in the ovary are accompanied by physiological changes that are equally profound. It is these physiological results which give to the functional rhythms of the ovary their importance.

THE ENDOCRINE MECHANISM OF THE CYCLE

This hastily drawn picture of the closely interwoven rhythms of growth and regression in the ovary and uterus, compounded of both morphological and physiological changes closely associated with external manifestations of oestrum in the lower mammals, would not be complete without some attempt to specify the mechanism which keeps the wheels going round. Fortunately the extensive as well as intensive work that has been occupying the time and attention of many investigators on hormones and their relations to the gonads, offers this explanation, incomplete though it is. So extensive has the literature on this subject become that

any attempt to give an adequate survey of it in a short paper is hopeless. The outstanding results only can be indicated.

Studies on the hypophysectomized rat (Smith, 1927, 1930) have shown, beyond a doubt, that the follicular-growth hormone of the anterior pituitary is the stimulus for the growth of follicles beyond a small size. A considerable amount of experimental work (Leonard, Meyer, and Hisaw, 1931, among others) also demonstrates the fact that the sex hormone of the ovary, or the folliculin secreted by the follicles which have reached a certain maturity is antagonistic to the hormones of the anterior pituitary, and, when present in amounts equal to that found in mature follicles, suppresses them, with a consequent lack of further growth in the follicles. Referring back to what has been said concerning the ovarian cycles in normal animals, it is found that the middle of the cycle sees the growth of many follicles, which must be due to the follicular-growth hormone, and that at the end of the cycle, when mature follicles are present, all of the follicles disappear, either through ovulation or atresia. This stoppage of follicular growth must be due to a cessation of output of the follicular-growth hormone by the anterior pituitary, and is evidently caused by the suppression of this function by the folliculin which has been produced in the ovary. The mature follicles thus form the agent by means of which the formation of the hormone upon which their own growth and well-being depend is suppressed, resulting in an almost total lack of growth at this period and atresia of all follicles already present. This, in turn, results in a drop in the amount of folliculin present, thus allowing the anterior pituitary to renew the production of follicular-growth hormone, starting a new cycle of growth in the ovary. The interaction of these two hormones, the follicular-growth hormone of the anterior pituitary and folliculin from the ovary, thus forms a self-regulating mechanism by means of which the physiological and morphological rhythms of the ovary and uterus are produced and maintained throughout adult life. This has been worked out in great detail by Moore and Price (1932) from the experimental side, and summarized for the normal animal by Evans and Swezy (1933).

With the suppression of the follicular-growth hormone, the luteinizing hormone of the anterior pituitary becomes active, with ovulation followed by the formation of corpora lutea. It seems quite probable that ovulation is caused by some other factor than the luteinizing hormone, but in the normal cycle these are not clearly separated.

Recent investigations (Swezy, 1933) show that the luteinizing hormone of the anterior pituitary has a depressing effect on the production of new germ cells in the ovaries of rats when this is given under experimental conditions. During the normal cycle this effect is shown by the lowering of the rate of ovogenesis at the time of ovulation when this hormone is acting in the ovary. The follicular-growth hormone seems to have less of this effect, hence the appearance of great numbers of new germ cells during the middle of the cycle when the greatest amount of follicular growth occurs. The results of the experimental administration of these hormones is thus confirmed by the conditions found during the ovarian cycle in the normal animal.

After an operative removal of the anterior pituitary (Smith, 1927; Swezy, 1933), which brings about an entire absence of all of these hormones, there is an entire absence of all rhythms in the ovary, with profound atrophy of the uterus. Atrophy

in the ovary is less complete, and is characterized by the absence of all medium and large sized follicles and corpora, the production of new germ cells continuing at an increased rate. Ovogenesis seems to be a continuous process after this operation with continuous degeneration among the ova, thus confirming the relation indicated between the hypophysial hormones and this process in the normal animal, as in the experimental animals which have received these hormones.

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MORPHOGENESIS OF THE SHOULDER ARCHITECTURE
PART II. PISCES

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HISTORICAL

MACLISE (1832) and Oken (1843) looked upon the limb girdles in the light of modified ribs. Owen was of the same opinion, but in addition he believed that the limb bones are homologous to such structures as the uncinate processes of the ribs of birds and branchiostegal rays. It was not, however, until after the middle of the century that the girdles came in for the share of attention which they merit. At this time Gegenbaur (1865) advanced the belief that not only the pectoral but the pelvic arch as well have developed from gill arches, the bones of the limbs proper representing gill rays. Davidoff, Fürbringer, Braus and others have held the same opinion. Parker, in various papers, has stated his belief that the pectoral girdle represents an extra-branchial cartilage—a more plausible contention. But the thesis that the appendages are derived from essentially branchial elements has never enjoyed the popularity of the so-called finfold theory, holding that the paired as well as the unpaired fins represent local remnants of continuous longitudinal fins. This theory was advanced independently and almost simultaneously by Thacher (1877), Balfour (1878), and Mivart (1879). In its essential features it has been accepted also by Haswell (1883), Dohrn (1884), Mayer, Wiedersheim (1892), Mollier (1893), Woodward, Harrison (1895), Dean (1896), Rabl (1901), Regan (1904), Goodrich (1906), Osburn (1907), Sewertzoff (1907) and many others. Many of the investigators on the subject, however, have failed properly to commit themselves whether they considered that the paired fins have had endo- or exoskeletal derivation. Among those who have definitely subscribed to nonaxial derivation have been Mivart, Cuvier, Huxley, Silliman; while Goodsir (1857), Macalister (1877), G. St. Hilaire, and Gregory believed that the fins have had a nonaxial or peripheral origin.

The theories of fin genesis will be further considered in future chapters.

APINNATE CHORDATES

It is desirable to call brief attention to the lancelet and cyclostomes because of the arrangement of their nerves and myomeres. Both are more highly specialized than is usually admitted. In *Amphioxus* there are dorsal myotomes with a basic appearance, for they are segmented and staggered diagonally, but the facts that ventral muscle fibers run transversely rather than axially and that these are innervated by the dorsal rami of the spinal nerves are utterly divergent from the vertebrate plan. The lack of a brain, the anterior extension of the notochord, and the presence of the atrium are further divergent features.

The Cyclostomata are, of course, very primitive in most respects and are thus useful in comparative anatomy, but they are very clearly degenerate and almost parasitical. Allen (1917) investigated the

spinal nerves of *Polistotrema* and found them basically primitive in that the dorsal sensory and dorsal motor branches are separate. This is true as well in the case of the more caudal of the ventral branches, but those more anteriorly have fused. In embryos of *Squalus* most of the sensory and motor nerves are separate also, and fusion takes place by peripheral union, this then progressing centrally.

FOSSIL PREFISHES

The known forms may be briefly considered in four groups as follows:

I. Paleospondyli, apinnate and of doubtful affinities.

II. Ostracodermi. Silurian and Devonian ostracoderms were the oldest known chordates (Gregory, 1915). The same author (1933) considers that ostracoderms as a class were the archetypal vertebrates from which were derived cyclostomes on the one hand, and gnathostomes on the other, but such a common ancestor must have been much more generalized than any ostracoderm yet discovered. Of the three orders the Heterostraci, apodial so far as known, may be excluded from consideration because the exoskeleton was of dentine rather than of bone. In the Osteostraci the exoskeleton was largely of bone. In the only family that is well known, the Cephalaspidae, there was an extensive cephalic shield and at least in some sorts there was a pair of anterior appendages, which, however, may not have been homologous to the pectorals of higher forms. Little is known of the shoulder architecture, but the limbs were probably used for the purpose of propulsion along the bottom by alternate action, and possibly for stirring up the mud in search of food. This would have involved antero-posterior rather than vertical movement of the limbs, and protractor-retractor musculature doubtless occurred. Additional details of Cephalaspids are mentioned in future chapters.

The third order usually considered as comprising the ostracoderms is the Anaspida, so grouped largely because there is no better position in which to place them. They were largely fish-like in form but appear to have been without paired appendages; and they had interesting, longitudinal rows of dermal scutes, ventrally placed, suggestive of similar structures in the sturgeon.

III. Antiarchi. This is an aberrant, highly specialized group, with a greatly developed, carapace-like shield of bony elements. There were club-shaped, anterior appendages but it is not known if these were strictly homologous with pectoral limbs. A group of high tangential specialization.

IV. Arthrodira. This group, with extensive joint between the shields of the cephalic and body regions proper, is of interest chiefly because some of its members appear to have had paired pelvic but no pectoral appendages.

The development of the tail in these prefishes is in a heterocercal direction, clearly indicating a bottom habitat. Some are without paired fins, in others there are pelvics, and in still others a pair which appears to correspond with pectorals, but in no sort known were both pairs present.

CHONDRICHTHYES

This group comprises the Elasmobranchii only, which may be divided into five orders (Bridge, 1922) as follows:

1. Acanthodei (extinct), comprising the acanthodians;
2. Pleuropterygii (extinct), including the cladoselachians;
3. Ichthyotomi (extinct), including the pleuracanthids;

4. Plagiostomi, including the sharks, Selachii, and rays and skates, Batoidei;
5. Holocephali, comprising the chimaeras.

Of these five the acanthodians occupy a pivotal position. Like so many other fossils the known forms are entirely too specialized to have occupied a directly ancestral position. Earlier, generalized members of the group may well have given rise to both the cartilaginous and bony fishes, although Bridge (1922) considered that the presence of shagreen tubercles indicated that they constitute a terminal offshoot of early elasmobranchs. At any

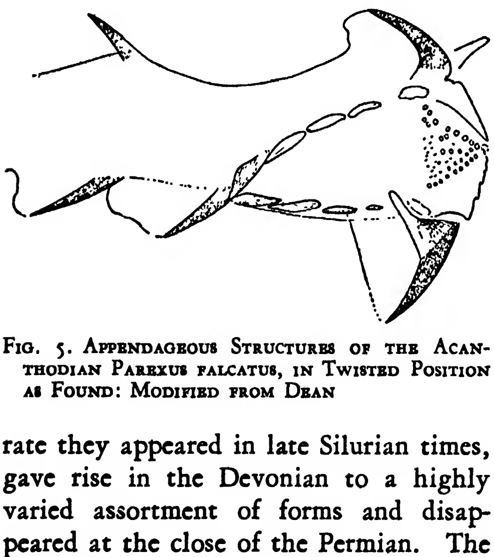

Fig. 5. Appendageous Structures of the Acanthodian Parexus falcatus, in Twisted Position as Found: Modified from Dean

rate they appeared in late Silurian times, gave rise in the Devonian to a highly varied assortment of forms and disappeared at the close of the Permian. The rows of dermal protuberances which some of them had are extremely significant. Thus, Dean (1907) figured and described the interesting genus *Parexus* (fig. 5), in which there was a row of heavy dermal spikes along (clearly) the branchiocloacal line. The anterior of these is greatly hypertrophied, with the posterior only slightly less so, and posterior from each there appears to have been a fin membrane. In this genus, as in others, there is thus dermal evidence of a true pectoral and a true pelvic fin, separated by a hiatus. In *Acanthodes wardi*, however, (fig. 6) there were no true pelvic fins, the second pair clearly having been directly in posterior sequence with the pectorals, as in so many living teleosts. So this group apparently elaborated fins of different sorts out of paired series of longitudinal dermal structures.

All Elasmobranchii, other than acanthodians, had both pectoral and pelvic (as opposed to ventral) fins. The pleuracanthids are not of great interest in the present connection. Cladoselachians are

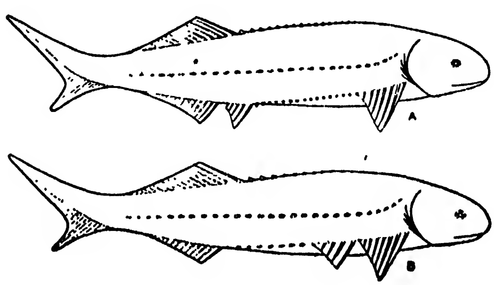

Fig. 6. Hypothetical Reconstruction of Two Ancestral Types of Acanthodians, with Longitudinal Series of Dermal Structures in Critical Areas: (A) Showing Early Development of Pectoral and Pelvic Fins; (B) Based on Actual Conditions in Acanthodus wardi, without Pelvics, but with Derivation of Ventral Fins from the Posterior Part of the Pectoral Element

the only certain representatives of the Pleuropterygii and are of particular interest because their fins have often been considered of extremely primitive type, chiefly because the radialia are relatively unconcentrated. As a matter of fact the fins appear to be much specialized, but in a manner that is unique among known forms.

The Selachii, or sharks, although exceedingly primitive in many respects, are far off the direct pathway that led to higher vertebrates. The exoskeleton is well developed but in a direction different from that taken by the direct line of

ascent, for the elements are discrete and occur in single dermal tubercles or placoid scales (shagreen) all over the body. Hence there are no membranous bones associated with endoskeletal cartilages, as must have been the generalized situation. The endoskeleton, too, with its slight calcification, exhibits a retrograde condition. Certain details of the muscles and particularly of the nerves of the more generalized sorts offer much evidence of significance, however, and these details are discussed elsewhere.

OSTEICHTHYES

This group contains all fish except the Elasmobranchii. No arrangement yet proposed is satisfactory in all respects, but the following may be used for the present:

Subclass Dipnoi—the lung fishes
Subclass Teleostomi
- Division Crossopterygii—lobe-finned ganoids
- Chondrostei—sturgeons and paddle fish
- Holostei—gars and bowfins
- Teleostei—true bony fishes

All the Osteichthyes have one character which is shared by the higher vertebrates and which is lacking in elasmobranchs, and that is the presence about the head of exoskeletal membranous plates which have become a structural part of the skeletal plan. Some of these are so arranged as to enclose the external gill aperture in a bony framework, and the posterior border of this forms a support for the developing endoskeletal structures. This, constituting the clavicular girdle, may maintain its original position largely at the surface of the body (sturgeon) but more often sinks beneath the surface, being grossly indistinguishable in the adult from bones of endoskeletal origin.

Dipnoans are in some respects very primitive, but in others, as the anatomy of the paired fins, dentition, and bones of the skull, they are highly specialized, and in a direction away from the main line of vertebrate ascent. It is likely that they arose from some of the more specialized crossopterygians (Regan, 1904). Of this group *Ceratodus* and *Protopterus* were dissected in the present connection.

The first three divisions of Teleostomi, consisting of Crossopterygii, Chondrostei, and Holostei, comprise the ganoids, and of them the second group is the most generalized in many respects, though not in all. Ganoids, like dipnoans, have both pectoral and true pelvic fins. *Polypterus* of the first group, *Acipenser* of the second, and *Amia* of the third were dissected during the present study. Of particular interest is the sturgeon *Acipenser*. It is certainly not an ancestral type and some of its specializations are quite extreme, but in its external details it offers evidence of much value. This involves the three longitudinal series of body scutes, along the middorsal line, lateral lines from head to tail, and from each pectoral to pelvic fin. The first and last of these are in the situations of the hypothetical fin folds of the fin-fold theorists and are believed to be relics of extreme significance. In addition the anterior border of the pectoral fin appears to have been derived directly from one of these scutes.

Polypterus is of importance in being the less specialized of the only two crossopterygian genera now living, and it was undoubtedly from the rhipidistian crossopterygians of the Palaeozoic that the early amphibians arose (Baur, Watson, Broom, Gregory), for these are the only fishes known having vertebrae, skull and limb bones of a pattern that could have been ancestral. The fins of the living representative have, however, become specialized in a tangential direction.

There are almost as many ways in which the Teleosti may be arranged as there are

ichthyologists for the reason that the interrelationship of some of the groups is very obscure. Boulenger (1922) divides them into thirteen suborders as follows:

1. Malacopterygii, including tarpon, salmon, grayling, smelt, herring;
2. Ostariophysi, including characins, catfish, carp, loaches, tench;
3. Symbranchii, eel-shaped fish without paired fins;
4. Apodes, eels;
5. Haplomi, including cyprinodonts, pike;
6. Heteromi, mostly deep sea fish;
7. Catosteomi, sea horses, sticklebacks;
8. Percesoces, gars, mullets, barracuda, rudderfish;
9. Anacanthini, cod, haddock, pollock, and many deep sea forms;
10. Acanthopterygii, about 80 families of perch, blennies, cichlids, wrasses, mackerel, flatfish;
11. Opisthomi, eel-like, aberrant forms;
12. Pediculati, anglers;
13. Plectognathi, trigger and trunk fishes, mola.

Some of the teleosts are, of course, quite fantastically specialized and of no use to us, and even the simplest are far from generalized. The fins of some, however, exhibit a simple arrangement of their musculature, this varying largely with function, as discussed later. Features of the paired fins of teleosts appear to suggest that they have been derived from at least two, and possibly more, distinct sorts of very early acanthodians or other ancestral types, one of these having only paired fins in the pectoral region, and the other both pectoral and pelvic appendages, as considered more fully elsewhere.

GENESIS OF THE APPENDAGES

In examining the evidence pertinent to the derivation of the paired fins, a consideration of the two major theories so far advanced is essential. These are the Fin-fold Theory and the Gill-arch Theory.

Fin-fold Theory

The controversy over this hypothesis, advanced first by Balfour and by Thacher, has waged long and bitter. In its most logical form it postulates that the paired fins of fish represent opposite ends of a pair of continuous fins originally extending from the gills to the cloaca, and that median fins are similar remnants of a single fin in the middorsal line which extended around the tail to the cloaca, the arrangement having been much as now occurs in *Amphioxus*. It has been vigorously supported by a host of investigators, as already enumerated, and as energetically denied by others. Much impressive evidence may be marshalled to its support, as was done by Osburn (1907), but most of this is capable of being interpreted in other ways. On the whole the arguments should be more broadly interpreted, and the derivation from an actual longitudinal fin less uncompromisingly stressed.

The chief argument, perhaps, of the fin-fold protagonists is that the azygos and the paired fins of fish are similar in structure. This is only to be expected, for they are formed in the same manner from the same materials. The chief argument against this theory as usually advanced is the fact that although there is a suggestion of an epiblastic fold along the back in such elasmobranch types as *Scillium*, *Pristiurus*, and *Torpedo*, and even lateral ones from the cloaca to the pectoral region (Daniel, 1922), a continuous, longitudinal fin is not a character of a generalized vertebrate with fusiform body, but of the anguilliform, specialized type. Continuous fins have been developed by diverse sorts of fish, but only as an accompaniment of elongation of the body, as has been mentioned several times by Gregory (1915 and later). Finally it

appears that the evidence that the basic plan of the fin musculature was antero-posterior, instead of dorsoventral, renders the acceptance of the fin-fold theory in its usual form an impossibility, for such a fin must be operated by antagonistic dorso-ventral groups of muscles.

Gill-arch Theory

The alternative to the fin-fold theory has heretofore been the hypothesis that the pectoral fin at least is a derivative of the branchial apparatus, the girdle representing the branchial arch, and the skeleton of the fin proper a modification of the branchial rays. Originally advanced by Gegenbaur, this theory has attracted many supporters, some of whom have carried their arguments to fantastic lengths, claiming that the pelvic fins are also pharyngeal developments. As in numberless other cases the endeavor has usually appeared to be the proof of a favorite theory rather than the discovery of the truth.

As brought out in subsequent pages some of the facts used in support of the gill-arch theory are incontrovertibly persuasive, but all such facts can be interpreted in different ways. Some of the usual counter-arguments also are based upon misinterpretation of facts. Thus the statement by Dean (1902) that the pectoral girdle of *Cestracion* shifts forward during embryonic development was utilized by Osburn (1907) as disproof of the gill-arch theory. Actually this fact is merely an indication that the most posterior of the branchial arches, once present in an ancestor, have become atrophied in this form and the girdle takes a more advanced position as a result. An argument against the gill-arch theory is the claim that the pharyngeal structures develop in the medial or visceral part of the mesoderm and the shoulder girdle in the lateral or somatic part. But the incontrovertible proof that this theory cannot be fact is the circumstance that the intrinsic muscles of the paired fins are all innervated by somatic rather than visceral nerves.

Position of the appendages

There are undeniably critical areas for the elaboration of special details in all primitive animals. The midline dorsally, then around the tail and anteriorly as far as the cloaca, and the branchiocloacal lines are such, for it is only along these that fins developed. Furthermore there appears to be no limitation to the situation along these lines in which fins may occur. They may be in two pairs, at the opposite ends of the branchiocloacal line (elasmobranchs, dipnoans, ganoids, some teleosts); there may be only a pectoral pair (some ostracoderms, antiarchs), only a pelvic pair (arthrodires), or two pairs derived from consecutively contiguous somites (some acanthodians, and seemingly some teleosts). Living fish give the appearance of having been derived from the first and last of these categories, as already set forth (Howell, 1933c). Among teleosts at least the Malacopterygii conform to the same fin plan as elasmobranchs, dipnoans and ganoids, having true pelvic fins in addition to the pectoral pair, at opposite ends of the branchiocloacal line, the former basically for support and the latter for locomotion. But the teleostean suborders Anacanthini, Acanthopterygii, Pediculati and probably Plectognathi are largely composed of groups which appear to be derived from ancestors having no true pelvics. Instead the innervation suggests that in these a need for stabilizing appendages was supplied by the posterior elements of the pectoral series, which migrated ventrally to form so-called

ventral fins in neurologic sequence with the pectoral pair. It even appears possible for three pairs of appendageous structures to be derived from the original pectorals, as illustrated by the genus *Polynemus*(figs. 7, 8). This suggestion in regard to fin homology can be established or disproved only after much lengthy research.

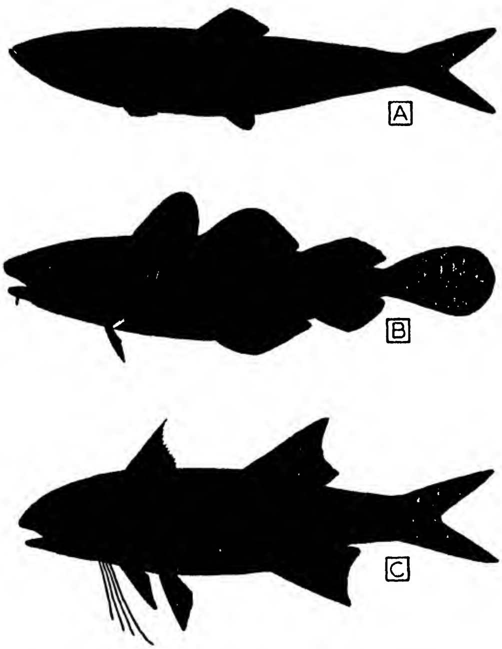

Fig. 7. (A) Clupea and (B) Gadus, Showing Diagrammatically the Dissimilarity in the Arrangement of Fin Nerve Distribution. (C) Polynemus, with 3 Anterior Paired Fins

The position of the fins can probably change within certain limits, and the position of a plurisegmental pelvic fin may, under particular conditions, simulate that of a ventral fin of few segments derived from a pectoral, but it is probable that such migration becomes severely restricted once the fin has become securely anchored to a girdle. The vertical position of the pectorals is also variable, these having assumed a position much higher upon the sides of some fish than of others.

Exoskeletal fin genesis

The belief is rather well established that the initiation of the fins was from dermal elements. As early as 1879 Mivart stated that paired limbs are essentially peripheral structures which have become more or less closely connected with the skeletal axis, while the limb girdles are

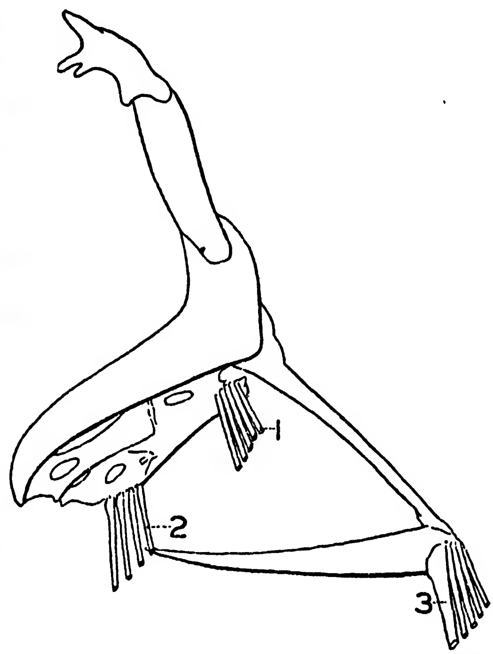

Fig. 8. Left Shoulder Girdle of Polynemus, with 3 Pairs of Anterior Fins: (1) True Pectoral, (2) Pectoral Filaments, (3) Ventral Fin

ingrowths from the bases of the limbs. Dermal fin rays are formed by fusion of lines of scales (in Actinopterygii) superseding the horny fin rays of an earlier period (Gregory, 1915); fin spines are clusters of metameric tubercles (Dean, 1907); and there are other similar statements in the literature.

Certainly fins could not have suddenly appeared as fins. There must have been a lengthy initial period during which they did not protrude sufficiently to be of use in locomotion, or in any other

definite action. It is likely that in the situations in which they later took form, along the midline and branchiocloacal lines, there were first series of longitudinal dermal structures of poor differentiation, and nothing is so likely as rows of scutes or enlarged scales, suggestive of those indicated in the apinnate anaspid *Birkenia*, and of the dermal structures that have now become hypertrophied in the sturgeon (fig. 9). Those scutes which were subjected to particular stresses during daily activities would naturally experience a stimulus for further differentiation, resulting in spines or rays that could have been used as props and as aids for wriggling over the bottom or for stirring up mud in search of food, and these are believed to have been the earliest definite

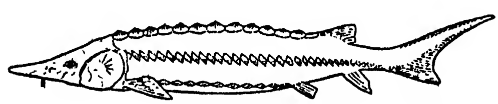

Fig. 9. The Sturgeon, Acipenser, Showing the Distribution of Longitudinal Dermal Structures

functions of paired appendages. That the first critical functions were concerned with a habitat upon the bottom is indicated by the fact that the basically primitive types of all fish phyla show a heterocercal tail. Unpaired fins could have developed for equilibration at any time.

The appendages may have first taken the form of a heavy anterior ray and several successively smaller ones posteriorly, as suggested by a number of acanthodians such as *Parexus*, and by *Acipenser* (fig. 10). This may well have been the plan followed by those vertebrates with limbs having few somites. Or the initial plan may have involved the rather uniform development of a considerable number of dermal rods, suggested by elasmobranchs, with more numerous somites. It is evident that the original dermal rods, or dermotrichia, may break up into a number of more slender elements, so that the rays may be much more numerous than the somites contributing to the fin. In elasmobranchs there is but a single layer of these, but they are double in Teleostomi.

It seems extremely probable that at first each fin was as broad as the number of somites entering into its composition, with the dermal fin rays parallel. At this stage considerable migration of the fins was probably possible, by means of hypertrophy at one end accompanied by

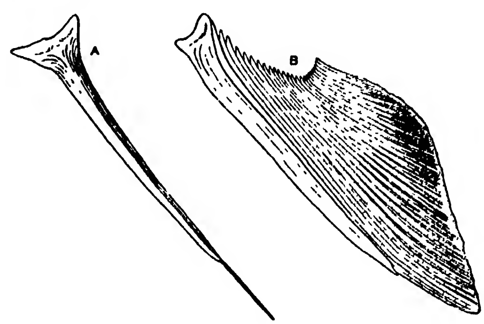

Fig. 10. Right Pectoral Fin of the Sturgeon Acipenser, Showing Hypertrophied Dermal Ray upon Preaxial Border: (A) Anterior, and (B) Ventral Views

a compensating atrophy at the other. Later, however, there was concentration at the proximal bases of the dermotrichia, for increased mobility, brought about by differential growth of fin and body (Goodrich, 1930), and then concrescence or partial fusion at the base of the fins, not of the dermal rays but of basal cartilages. After this became at all pronounced any marked migration of the fins, at least to a greater extent probably than a very few segments, is considered to have been unlikely.

Stimulation by diverse uses

Before taking up specific anatomical evidence encountered in living fish, it

should be mentioned that after the paired fins became developed to the point where they were really of primary use to the animal they started to become further modified in a variety of directions, according to action. Such uses are of distinct sorts, as follows: (a) For propulsion over the bottom by appendages of the crutch-prop type: (b) As a horizontal rudder, much as an immobile dorsal fin is employed, a fairly primitive function, used, probably more or less exclusively by *Cladoselache*, and to a modified extent by recent sharks; doubtless correlated with the fact that sharks are prone to turn upon the back when grasping food: (c) Chiefly for vertical ascent or descent, by tilting: (d) For turning by means of the unilateral braking action of one out-thrust fin, as employed by most teleosts: (e) For propulsion oarwise, not utilized in speedy progression: (f) For fanning movements of the pectoral pair in aiding the flow of water through the gills; a specialized development of many teleosts: (g) For counteracting, by means of tilting of the fins, disturbance of equilibrium by water ejected through the gills; often an important function: (h) As simple props, to maintain an upright position when resting upon the bottom: and (i) for such functions as claspers, in correlation with reproductive processes. In addition fins are often highly modified for a variety of uses such as feelers, which tend to change them from a pinnate form. For (a) and (h) a spike-like fin would be most efficient; for (b) and (c), involving vertical steerage, a broad-based fin of the selachian or even the *Cladoselache* type; and for the remainder a fin with constricted base but with its plane tilted in various ways. This question of tilting has a pronounced effect upon the controlling musculature. Regardless of the position finally adopted preaxial and postaxial, dorsal and volar (if such a term be permissible in fish) is employed to denote the respective morphological aspects of the appendage.

ANATOMICAL EVIDENCE IN LIVING FISH

Pharyngeal evidence

Visceral details have had much influence upon the anterior limbs and must be considered. It may be accepted, I think, without going into particulars, that the entire oropharynx and branchial equipment innervated by the tenth nerve belongs with the viscera. It is also evident that the branchial segments pushed out between the lateral and ventral divisions of the somites, the original displacement of the latter perhaps having been helped by the development of the pronephros (Agar, 1908). It further seems evident that in some, if not all, of the earliest fish a greater number of posterior branchial arches was elaborated from vagus elements than is now found in their descendants, as indicated by the facts that in some elasmobranch embryos rudimentary gill arches occur posterior to the functional set (Daniel, 1922), and that in some forms there is a slight anterior migration of the pectoral limb during ontogeny (Dean, 1902). Nevertheless the pectoral appendages have been much displaced in a rearward direction, chiefly by the development of the gills, and they never regained their original position.

The cartilaginous gill arches have but slight interest for us in the present connection, but some of the pharyngeal muscles do have. In all fish one or more of the gill muscles, innervated by the vagus nerve, has posterior insertion upon the scapulocoracoid girdle in elasmobranchs, or upon its analogue, the clavicular girdle in other fish. Presumably in the tetrapod ancestor there were two

such muscles, one dorsally, representing the future m. trapezius, and the other ventrally, the precursor of the m. sterno-cleidomastoideus. In the dogfish the dorsal component alone is represented. It is in seeming series with the mm. interarcuales laterales, of the branchial series, farther forward. In bony fishes there are usually additional branchial slips attached to the girdle. In the cod

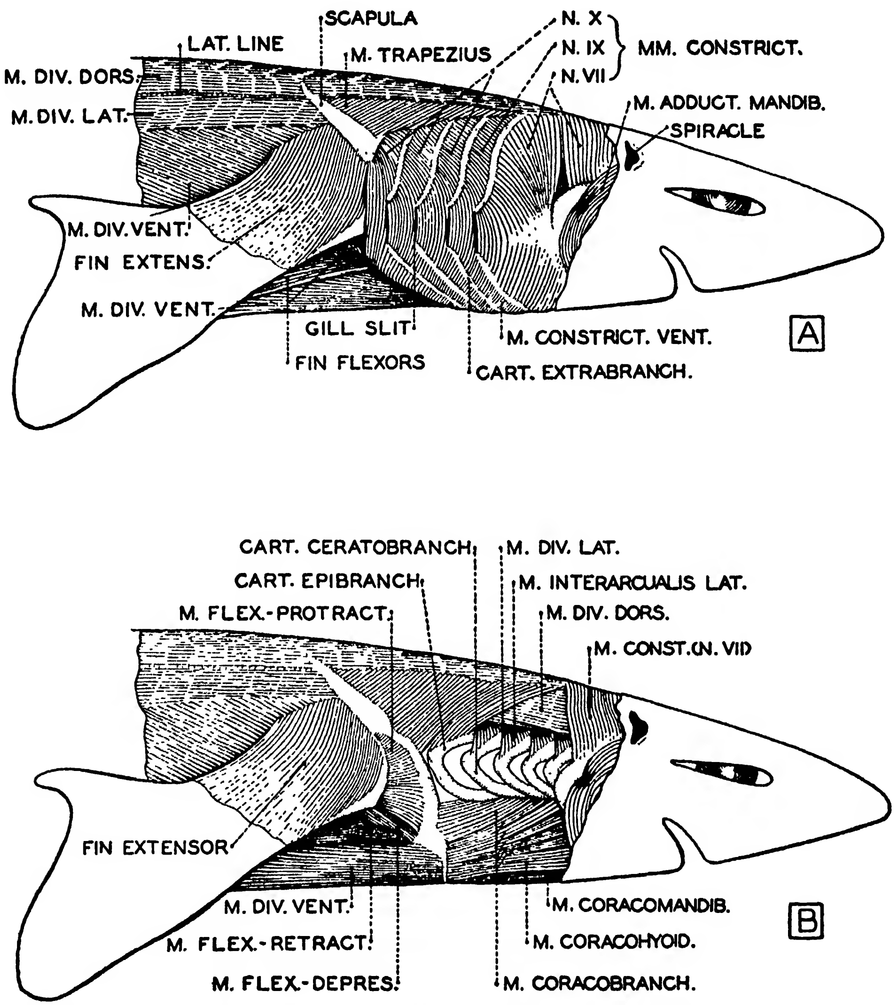

Fig. 11. Musculature of the Dogfish (Squalus acanthias) in the Region of the Shoulder: (A) Superficial Aspect, and (B) Deeper View of Branchial Details

It originates from the skin and fascia covering the suprascapular part of the dorsal division of trunk musculature (fig. 11), and extends ventrocaudally to insert upon both the epibranchial cartilage of the last gill arch and the anterior border of the ventral half of the scapular cartilage. (*Gadus*), for instance, two slips converge to the girdle from above and below, these being so situated as to suggest homologues of mm. trapezius and sternocleidomastoideus. In addition small branchial slips are at times attached to the dorsal part of the clavicular girdle. It is doubtful,

however, whether such slips can be homologized in different groups of fishes. The literature is confusing on this subject, for authors have frequently assigned the term trapezius to somatic muscle slips without vagus innervation.

The history of the gill apparatus in morphology has been for the posterior development of the hyoid usually to form an opercular covering, overlapping and protecting the entire series of gill clefts beneath it. As a result there was reduction of the branchial septa and a progressive restriction of the opercular orifice. When branchial respiration becomes reduced, as in *Lepidosiren*, the arches tend to revert to an unsegmented condition and the next step, in amniotes, is the disappearance of the opercular opening. As the gills disappear so do their controlling musculature and the branches of the vagus nerve going to them, except for the branch to the posteriormost of the series, which bersists in higher vertebrates. In consepuence this part of the vagus gets left behind, cut off peripherally from the remainder of the nerve, and is known in tetrapods as the ramus lateralis n. accessorius.

Skeletal evidence

Pectoral girdle of elasmobranchs. It must be fully realized that whatever may have been the condition in the ancestral form presumably common to both sharks and bony fishes the girdles of these two groups have been elaborated on plans so different that they can hardly be compared, detail by detail, although the skeletal features, as a whole, have the same functions in both. It seems likely that the common ancestor of the two groups had exoskeletal appendages, but it is not improbable that it had not as yet established endoskeletal anchorage for the controlling musculature.

There are at least four possible factors that have been influential in the development of the anterior girdles: (a) somatic, concerning the trunk proper, (b) exoskeletal, (c) branchial, and (d) the possible effect of the intestinal viscera.

The fact that in bony fishes there are both clavicular (dermal) and scapulocoracoid girdles, while in elasmobranchs a single cartilaginous girdle fulfils the functions of both, makes a separate discussion of these two groups essential.

In order that trunk musculature, operated in swimming to move the tail in the horizontal plane, may operate effectively it must have firm anchorage anteriorly. Dorsally the attachment is upon the head in both groups, but laterally two sets of conditions obtain in elasmobranchs and bony fishes. In the dogfish, lacking dermal bones, the ventral somatic musculature reaches the head (mandible) as well as the gills, but laterally the postcephalic space is occupied by the gills, and a septal structure between these and the body musculature is furnished by the scapulocoracoid cartilage alone. This also provides a septum between the ventral division of the body musculature and the hypobranchial group, which, because of the difference in the functions of these two components, appears to be a necessity.

The exoskeletal influence upon the pectoral girdle is, of course, profound but not necessary for its existence. A fin of the type occurring in modern selachians is in mechanical need of an endoskeletal base for articulation, as well as to furnish origin to its musculature. *Cladoselache* must have had such a fin base anchorage, else the cartilaginous radialia could not have reached the degree of development which they did.

An additional stimulus operating upon the pectoral girdle of elasmobranchs is that of posterior anchorage for the branchial apparatus, and as a strut be-

tween the dorsal and somatic divisions of the trunk, in order that the gills may not be squeezed between them. In this

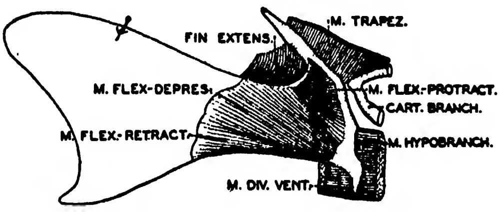

FIG. 12. MUSCULATURE OF THE VENTRAL SURFACE OF THE PECTORAL FIN, WITH PREAXIAL FIN BORDER ELEVATED, OF SQUALUS ACANTHIAS

means of the septum transversum, dividing the pericardium from the metacoele.

In the dogfish (as in *Heterodontus*) the girdle consists of a U-shaped cartilage continuous in the midventral region, but in *Heptanchus* it is there separated by an unpaired sternal cartilage (Daniel, 1922). In the sharks the girdle is free above but in the rays the points may be attached to each other or to a vertebra. The angle of slope varies much in different groups. In elasmobranchs the girdle is designated scapulocoracoid merely for convenience,

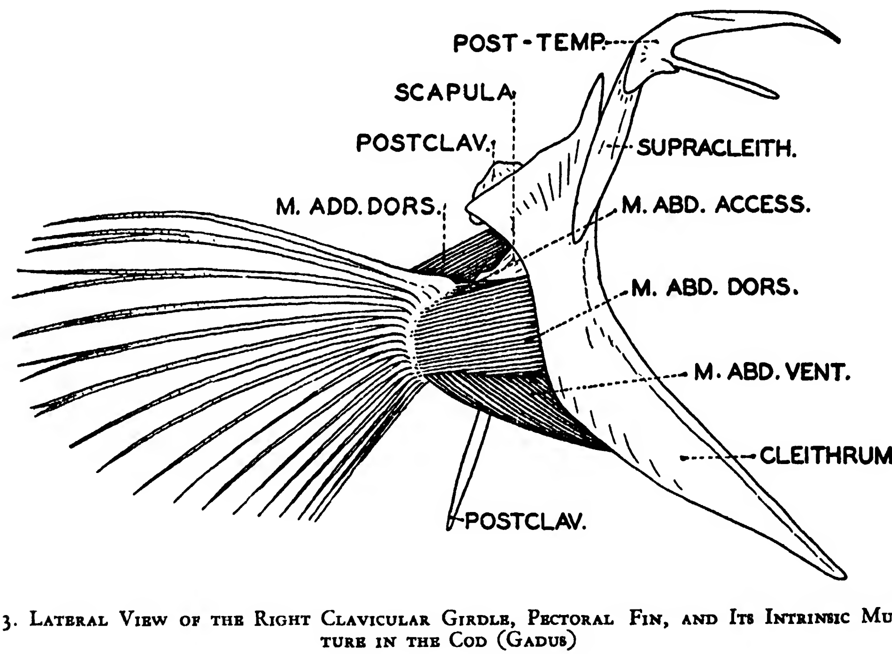

FIG. 13. LATERAL VIEW OF THE RIGHT CLAVICULAR GIRDLE, PECTORAL FIN, AND ITS INTRINSIC MUSCULATURE IN THE COD (GADUS)

group too, although it is believed that the pectoral girdle would be present even were there no paired fins, the former has undoubtedly been much modified and strengthened by the action of these appendages, in furnishing attachment for the intrinsic muscles. The fourth stimulus, of unknown strength, that has operated upon the selachian girdle is correlated with the fact that it affords attachment for the anterior viscera, by

for it is not entirely homologous with the scapula and coracoid of bony vertebrates. In the dogfish the only movable joint to the girdle is at the juncture of the dorsal with the lateral group of trunk musculature, where a small suprascapular cartilage articulates with the dorsal end of the scapula (fig. 13). The part of the selachian girdle just below the fin joint is pierced by the coracoid foramen (sometimes by a second) through which pass

the diazonal nerves supplying the original protractor musculature of the fin.

The pectoral girdle in bony fishes. In the bony fishes, as in the piscine ancestor of tetrapods, the very different basic conditions involved an extensive array of dermal bones, mechanically perfected probably before the appendages had had endoskeletal effect. Hence it is believed that this system, rather than the cartilaginous components as popularly stated, really constituted the primary girdle. Elements of this dermal system finally in teleosts the dermal elements typically present are post-temporal above, supracleithrum, and cleithrum below, although supernumerary bones occur in some sorts. This dermal girdle may be called analogous to the cartilaginous girdle in elasmobranchs, but there is this difference in function: in the latter group the girdle is interposed between the body musculature and the hypobranchial group, while in the majority of bony fish there is a postclavicle (fig. 14) so-called, generically variable in development, which in such a

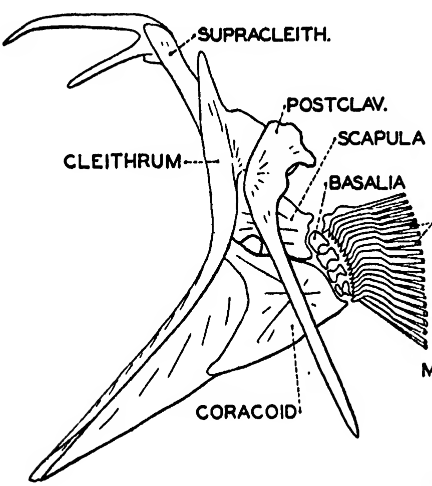

Fig. 14

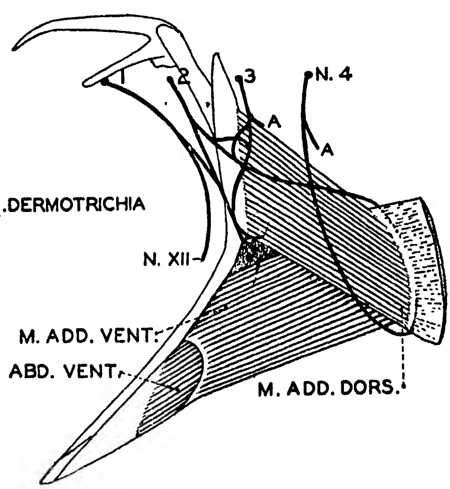

Fig. 15

Figs. 14 and 15. Medial View of the Right Clavicular and Scapular Girdles of the Cod (on Left). Medial View of Intrinsic Musculature in the Cod, with Distribution of the Brachial Nerves; Postclavicle Removed; (AA) Nerve Branches to Myomeres of Trunk (on Right)

came to encircle the gill openings, both for protecting the gills with the help of the operculum, for furnishing support for the branchial structures, and to provide necessary anterior anchorage for the body musculature.

This so-called clavicular girdle in the bony fishes is composed of elements that vary considerably in the major groups. Both clavicle and cleithrum occur in Crossopterygii, Chondrostei, and Dipnoi, but in Holostei and Teleostei the clavicle has been lost (Gegenbaur, 1895), so that form as the cod more nearly resembles a first rib in that it has developed in a myoseptum between the trunk muscles proper and the hypobranchial musculature, the latter having anterior attachment to the cleithrum, or clavicle when present. Above, the much reduced lateral trunk division is attached to a dorsocaudal process of the postclavicle. In bony fishes the clavicular girdle first provides attachment for the posteriormost of the branchial series, the homologues of the mm. trapezius and sternocleidomastoideus

in the tetrapod ancestor at least, and these latter appear to have shifted, at a later date, to the developing cartilaginous girdle. In the postpiscine stage the closure of the opercular opening and disappearance of internal gills was rapidly followed by the reduction of the encircling dermal shield and the clavicular girdle became incomplete, almost disappearing in higher tetrapods.

In this group it is considered that the cartilaginous elements of the scapular girdle had little or nothing to do with the clavicular girdle at first, being merely contiguous, the connection then being by soft tissue and only considerably later by articulation, as the cartilaginous increased in size and importance in inverse ratio to the dermal girdle. It seems likely that these elements in teleosts, rather than being secondarily reduced, never were larger than at present. They were initiated in intermuscular septa and marked points of divergent muscle stress. Primarily, in existing bony fishes as in the tetrapod ancestor, there is a more dorsal element termed scapula and a more ventral called coracoid. These are convenient terms to employ, but it is not certain that the two are precisely homologous in all bony fishes and tetrapods. After all, they merely mark points of antagonistic muscle stresses and may or may not be equal to the same thing in all cases. Some groups of Teleostei (Malacopterygii, Ostariophysi) have an additional element of the shoulder known as the mesocoracoid. Neither should an attempt be made to homologize this element with any structure in tetrapods, nor even, perhaps, with the so-called mesocoracoid arch of Holostei and Chondrostei, although the homologue of the latter does seem to occur in some of the lower tetrapods.

Foramina in the scapula girdle of ganoids, or Actinopterygii, consist of the coracoid, glenoid, and supraglenoid foramen, as discussed by Romer (1924). The first of these is for the transmission of the diazonal nerves and is of great morphologic value in vertebrates, but it is doubtful whether the other two are of broad phylogenetic significance. The homologue of the coracoid foramen in teleosts is the fenestration between the scapula and coracoid.

Consideration of the anatomical details of existing dipnoans and ganoids, even including *Polypterus*, shows that specialization of the fin and girdles has progressed too far in tangential directions for us to gain from them alone a proper idea of basic conditions, but the muscles, and often cartilaginous muscle canals, indicate much modification of a sort that was hardly followed by the main tetrapod line.

Appendageous skeleton in elasmobranchs. Before discussing selachians in particular the fact must be mentioned that there are two main schools of thought in regard to the line of evolution of the appendageous skeleton, one of which follows the hypothesis that it has developed according to the biserial, archipterygium plan of *Ceratodus*, occurring in early Dipnoans, crossopts, and *Pleuracanthus*, as advanced by Gegenbaur and followed by Gunther, Braus, Huxley, Howes and others, or according to the pleurorarchic plan, with basal axis, and radials along the outer edge, as Wiedersheim, Regan, Woodward, Sewertzoff and others have believed. Either thesis can be argued with plausibility, according to the ideas suggested in figure 16. It is rather likely that there developed a bar-like series of cartilages at the base of the primitive, unconcentrated fin (fig. 16, B) which could evolve in both directions. From a fairly generalized stage (fig. 16, D) could have come

possibly *Polypterus* (although its resemblances are probably of a convergent nature) and probably the arrangement most typical of selachians, involving three basalia comprising propterygium anteriorly, mesopterygium, and metapterygium posteriorly, articulating with the girdle. The embryonic condition bears out this sequence, for there is at first a single cartilaginous bar representing the metapterygium from which extend radialia; the bar seems later to become the main axis secondary to which arises the meso-, and finally the propterygium (Daniel, 1922), the smallest and apparently the most recent of the three elements. Gegenbaur and Woodward also considered the metapterygium as the main axis, although Huxley, Balfour, and Howes especially, have maintained that this rôle is filled by the mesopterygium. Goodrich considers that such precise commitments are unwise, and as a matter of fact there may never have been strict uniformity among the different groups. Thus in *Heterodontus* the propterygium appears at times to be fused with the mesopterygium, and occasionally, in a species of *Scymnus*, there is only a single basalium (Daniel, 1922).

The possibility must be entertained that the structure at the base of the pectoral fin in the remains of *Cladoselache* was nephritic rather than cartilaginous. At any rate, however, it must have had basal cartilages, and the discrete nature of the fin base suggests that these may have had a longitudinal form. The fact that the dermotrichia, if actually present, were relegated to the posterior border of the fin in cladoselachians, and the great development of the radialia indicate not only that the musculature was well developed, but also that the entire fin

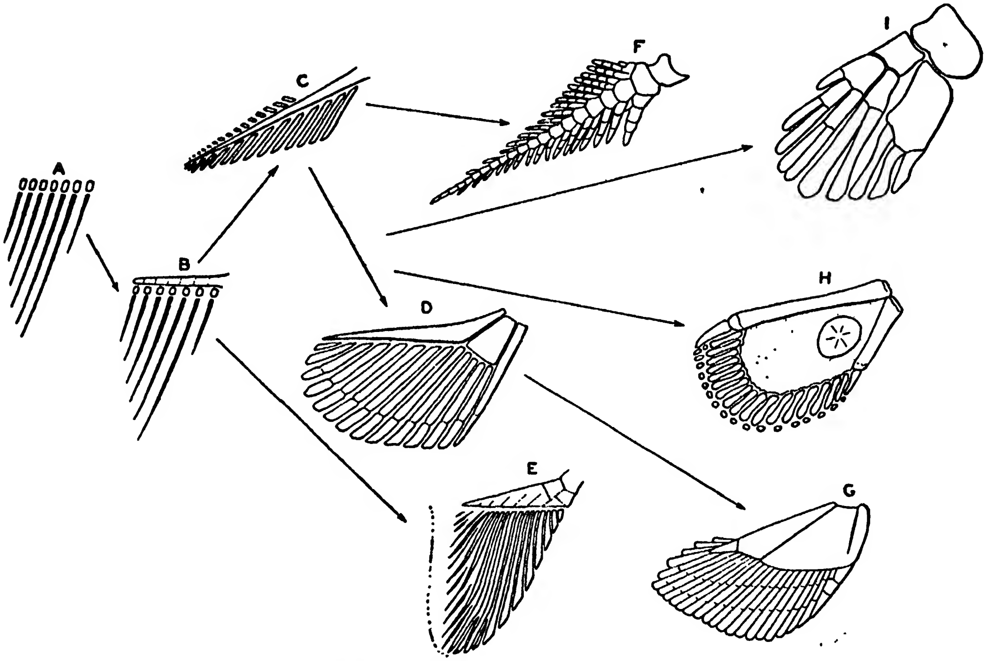

FIG. 16. HYPOTHETICAL MORPHOGENESIS OF THE PECTORAL LIMB IN FISH: A, B, C, D, HYPOTHETICAL STAGES; E, CLADOSELACHE; F, CERATODUS; G, SQUALUS; H, POLYPTERUS; I, SAURIPTERUS. PREAXIAL BORDER OF THE FIN TOWARD THE RIGHT

equipment exhibited a definitely specialized condition in all features except the unconcentrated bases of the radials, instead of a basically primitive one as usually claimed.

Typically the selachian propterygium distally bears but one (occasionally two) large, proximal radialium while the other two bear many. This row of radialia is distally followed by two more rows, the most distal of which appears usually, if not invariably, to consist of a number twice as great as that of the nerves supplying the fin. The radials arise not as outgrowths of the girdle but as differentiations of the mesenchyme in situ (Balfour, Ruge, Swinnerton, Derjugin).

In selachians the joint with the fin base is a simple articulation enclosed by a virtually continuous, fibrous capsule permitting more movement in the axial than the vertical direction, but in most bony fishes there is no true skeletal joint at this point, the elements not being sufficiently approximated.

As already stated the single layer of dermotrichia in selachians has been derived from a variably considerable number of body segments, and it is personally considered likely, although by no means certain, that the anteriormost was never much heavier than the others in this group. In fact it seems likely that the dermal element that was originally anteriormost in this group has disappeared, as explained in connection with the musculature.

Appendageous skeleton in bony fishes. The earliest types of bony fishes had a fin essentially of the biserial pattern, but hardly in its extreme form as now encountered in *Ceratodus*. This type of fin is suited to a rather sluggish life on the bottom, not to a predaceous, active, free swimming existence, which tends to develop a uniserial fin. Among fossil fishes the only group that fulfills the anatomical requirements necessary in the tetrapod ancestor is the rhipidistian crossopterygians, with what may be called a generalized biserial fin. Thus the fin of *Sauripterus* (fig. 16, I) and to a lesser extent of *Eusthenopteron*, provides us with a very satisfactory plan for the elaboration of the tetrapod limb. A discussion of the significance of this pattern belongs more strictly in the chapter on amphibians than here, however. The pectoral appendage of living crossopts may be considered as uniserial now, but it is believed to have become secondarily so, through shortening and loss of a humeral segment.

The most useful fin for a fish of active, free-swimming habits is one with an extremely short base, and a uniserial appendage of this pattern is the one encountered in all living bony fishes except dipnoans. Although the basal cartilages may be of some considerable length, especially posteriorly (as in *Acipenser*), they are located within the body contour (with *Polypterus* and a few aberrant sorts as partial exceptions) and more frequently take the form of a single row of insignificant nodules between the girdle and dermal fin. So this feature of the teleost fin base is believed to have degenerated from an ancestral condition involving moderate development in the biserial direction.

Swinnerton (1906) found that in the teleost *Gasterosteus* there is an embryological tendency for the glenoid line (fin angle) to rotate from a nearly horizontal to a vertical position. This tilting occurs in response to a variety of functional stimuli, as already mentioned, and the direction is typically one that involves elevation of the preaxial and depression of the postaxial border. As a result the "volar" aspect of the fin, in sorts in which this tilting has occurred, is di-

rected laterally and the dorsal surface medially.

The course of development probably followed in bony fishes by the dermotrichia has already been outlined, and mention made of the probability that the plan involved the original hypertrophy of one of the anterior dermal spines, which were fewer in number than in selachians. A circumstance needing interpretation is the fact that in bony fishes the dermotrichia occur in two layers. In *Polypterus*, say, it is possible that this could have been achieved by alternate staggering of the elements of an originally single layer, but this possibility can not be entertained in the case of teleosts, in at least many of which nerves pass between the two layers from each fin border. To explain this it seems necessary to postulate that either the dermotrichia are derived from two parallel rows of dermal scutes, which is not likely, or else that the scutes of the single row, in the ancestral condition, had bifurcated bases, which later became accentuated.

Neurological evidence

Most of the evidence based on the nervous system has already been discussed and repetition here would be useless. There are a few additional details to be considered, however.

It is clear that the fin musculature was derived from a number of body segments that theoretically was precisely the same as the number of spinal nerves entering the extremity, although in the course of phylogeny it is not inconceivable that one or two of these might be relinquished as the need arose. In practically all living vertebrates, however, there has been a concentration of the fin base, to increase mobility and effectiveness, and after this concentration became pronounced it is believed that the number of nerves supplying the appendage was fixed, at least within very narrow variational limits, for all time.

Constriction of the fin base started posteriorly and progressed forward. As a result the nerves entering the fin are gathered together at the fin base, the posterior elements of the series having a forward inclination to this point. But the entire fin has been displaced in a caudal direction by the development anterior to the girdle of the branchial apparatus, and so the anterior brachial nerves are also inclined, but to the rear.

It is believed that the variation in the number of brachial nerves in fish, especially elasmobranchs, is not a late development but reflects the fact that the basic ancestors of these diverse types elaborated their appendages out of a variable number of body segments, and that the only late change in the number of nerves entering the limb might be brought about by the constriction or expansion, within very narrow limits, of the corresponding motor nuclei in the cord.

In elasmobranchs a variable number of spinal nerves supply the fin and these are always more numerous than in bony fishes. In the dogfish (*Squalus*) they usually number ten, and are arranged in beautifully simplified manner, practically free from anastomoses (fig. 17). Typically the three anteriormost nerves pass through the coracoid foramen to the lateral surface of the fin and supply the protractor musculature—the anterior part of the flexor group. Posterior to these diazonal nerves the remainder of the brachial series supply all the extensor and the rest of the flexor musculature. Each of the brachial nerves except those of the diazonal group contributes a small branch to the corresponding trunk segment.

In living fish other than elasmobranchs the typical number of spinal nerves supplying the pectoral limb appears to be four or five, but the exact nervous pattern varies according to group to such a degree that it is impossible to pick any one as basic. Even in *Polypterus* the secondary specialization has likely been sufficient to obscure the picture probably typical of the generalized crossopterygians. Neither is electrical stimulation of the nerves of definite help, for the results are too diffuse in character to indicate the precise segmental origin of the muscle divisions.

other flexors, and those belonging to the remainder of the extensors. I regard it as impossible, however, to homologize these with the suprascapular, extensor, and flexor nerves of the tetrapod limb (Romer, 1924), for the respective muscle divisions supplied by these nerves vary too much even within the single class Pisces.

Myological evidence

In several selachians that have been investigated it has been found (Dohrn; Braus, 1899; Goodrich, 1906) that each trunk myomere gives rise to a pair of

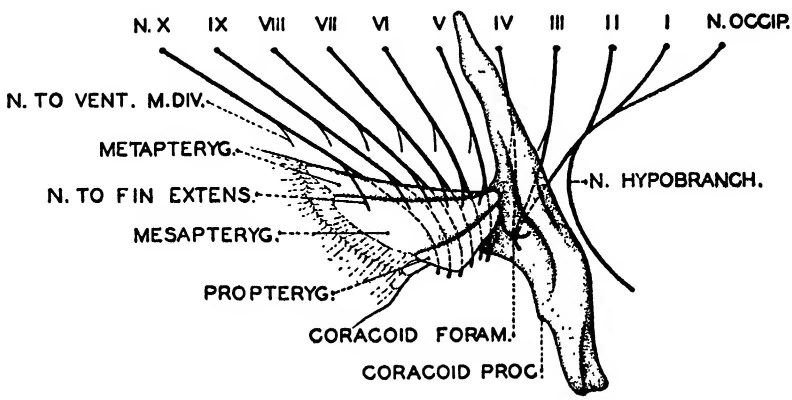

Fig. 17. Distribution of the Brachial Nerves of the Dogfish Squalus in Relation to the Girdle and Appendage of the Right Side

In some fish (as *Polypterus*) the first brachial nerve appears to supply only the flexor (protractor) musculature of the fin, while in others it innervates both extensor and flexor components. The diazonal nerve branches, passing through a fenestration between scapula and coracoid bones, appear to be derived from the first nerve only in some fish (as *Amia*), second only (as *Polypterus*), first two (as *Cyprinus*), or first three (probably most fish, as in *Gadus*).

The brachial nerves of fish may be grouped into those that pierce the coracoid foramen, the branches that supply the

muscle buds along the line of the paired fins. Those buds destined to take part in the fins develop and the remainder disappear. The latter may be interpreted as vestiges representing muscle slips which originally inserted upon a continuous series of dermal structures along the branchiocloacal line. It seems certain that the initiation of the appendageous musculature was in the form of a slip from each involved body segment to the corresponding dermal element, and that later these aligned themselves into a muscular complex for retraction and another for protraction. The latter group

could have been derived in a manner suggested in figure 4 of Part I, by secondary atrophy of the anteriormost dermal structures and attachment of their muscle slips to a more posterior ray, or else protractor slips might have differentiated entirely independently. At any rate it seems clear that longitudinal fission into a dorsal or extensor group and a ventral or flexor group came only later, as there was experienced need for the operation of the fin in these two directions.

The nerve distribution in the dogfish shows that in this selachian, as doubtless in others, all of the original protractor musculature contributed only to the flexor group now existing, and that the posterior part of the flexor and all of the extensor complex are derived from the original retractor slips. That the fin musculature of other fishes, including tetrapod ancestors, has also been derived from an original series of retractor and protractor muscles can hardly be doubted, but the plan followed may have been different from that obtaining in selachians. In some fish (*Polypterus*) it is true that the first brachial element appears to have contributed to the flexor musculature alone, but in most sorts both flexors and extensors are supplied by the first as well as subsequent brachial nerves. Unfortunately the picture in bony fishes, although at first glance simple, has passed through too many phases to be interpreted with certainty. It can merely be said that the longitudinal splitting of the retractor-protractor series into extensor-flexor groups may well have been determined on a more uniform basis than in the selachians by the fact that in bony fishes the dermotrichia occur in two layers, with nerve between, suggesting that the original dermal elements may have had a tendency toward bifurcation at the base, this feature largely determining the later division of the musculature.

In the bony fishes there occur, in different sorts, several slips with vagus innervation inserting upon the clavicular girdle, and it seems unwise to attempt to homologize any of these with trapezius and sternocleidomastoid of tetrapods.

In the dogfish the alignment of the intrinsic pectoral fin musculature is into a single extensor component, and three, or even four, flexor divisions, all of which are arranged to good advantage for moving the member in four directions. It is seen in the fresh specimen that the flexor divisions are alternately red and white in color, suggesting a difference in function such as obtains in the case of red and white muscle fibers of mammals. It is, therefore, not impossible that the actual differentiation of muscle divisions from a common plurisegmental mass was first determined as much by quality as by the direction of required movement. It was also found in the dogfish, by electrical stimulation of the brachial nerves, that each of these supplies a consecutively smaller muscle area progressing posteriorly, so that the area affected through the ninth or tenth nerve is but a couple of millimeters in width (Howell, 1933a).

In *Ceratodus* the fin musculature is entirely too complex to be indicative of a basic pattern, in *Protopterus* the intrinsic system is too degenerate, and in the other bony fishes it has probably been secondarily simplified to confusing degrees. One of the chief difficulties has been introduced by the tilting of the fin experienced by most bony fishes. In a teleost with simple fin action such as the cod (*Gadus*), the typical scheme of muscle arrangement involves a superficial and a

deep flexor (abductor), the two converging at an angle, and similar extensor (adductor) divisions, in addition to one or two small, accessory muscles. These presumably act to expand and fold the fin, as well as to abduct and adduct it. It is as simple an arrangement as could be really effective, but has evidently been evolved from a more elaborate pattern. Instead of a fin with elongate base, such as in *Ceratodus*, a free-swimming, active type of fish demands paired fins of extremely short base, and the modern type of teleost fin has been the result.

In response to functional requirements of one sort or another the pectoral fins in many teleosts have become tilted or rotated so that the border originally preaxial has become elevated and the postaxial depressed. To keep pace with this alteration in fin plane and to accomplish the work necessary the muscle origins have migrated to a greater or lesser degree. Thus the anterior or more superficial divisions of both flexor (abductor) and extensor (adductor) muscles have moved dorsalward (the latter a greater distance), and the two deeper divisions of both groups somewhat ventralward, instead of the extensors being above and the flexors below the fin. All four muscles are really more intimately concerned at origin with the cleithrum than with the cartilaginous girdle, but in addition the scapula now furnishes attachment to one extensor and one flexor, and the coracoid to the other extensor and second flexor.

The latter circumstance introduces a serious problem into the history of the shoulder girdle. It hinges on the question of whether the piscine forms ancestral to tetrapods had pectoral fins already tilted to the vertical position, or whether the originally horizontal posture of these members persisted throughout the aquatic period. If the former were the case then some of our accepted concepts of bone-muscle relationship in the shoulder would need revision. The point can only be decided after a study of conditions in postpiscine stages.

In *Polypterus* a third muscle element—a dilator, so-called—occurs in both abductor and adductor groups, as is also the case in many teleosts, but in the former genus the basal elements of the fin have degenerated and the muscular condition can not be considered as basic. On the whole the arrangement is not essentially different from that typical of teleosts.

Extrinsic muscles of the shoulder, in the form of slips from the trunk to various parts of the girdle, are better developed in the sturgeon than in any fish dissected. They are poorly represented in all, though, and lacking, as separate divisions, in most. They can appear in response to such a variable number of stimuli and in so many patterns that their plan in individual instances is totally without interpretable significance.

As already indicated much that is of use in the study of higher forms can be gained from the details of the skeleton in fish, and much from the nerves as well. From the muscles, however, not so many dependable facts can be gleaned, for it is doubtful that the plan now encountered in any living fish reflects conditions in the immediate piscine ancestor of tetrapods. One can with ease divide the muscles of the pectoral fin of all groups of fishes into prime movers and their antagonists, or the usual flexor-extensor scheme, as has been done in the past, but the derivation of these elements, segmentally considered, is so diverse in different fishes, that such division on a functional basis can have no homological meaning.

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THE FUNCTIONAL COMPONENTS OF THE DORSAL ROOTS OF SPINAL NERVES

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THERE has been considerable dispute in regard to the allocation of credit for elucidation and physiological demonstration of the law of the roots (Fulton, '30, pp. 251 and 258). Likewise the validity of this law has been challenged and questioned in relation to both the dorsal and ventral roots. It has been suggested that, in addition to carrying afferent impulses to the spinal cord, the dorsal roots serve as pathways for efferent impulses to skeletal muscle, blood vessels, other viscera and the sweat glands, the so-called spinal parasympathetic pathways. The evidence for and against such conduction to skeletal muscle has been reviewed by Ranson ('29). There is no question but that stimulation of the dorsal roots produces vasodilatation but the evidence which Bayliss ('02), and Fofanow and Tschalussow ('13) presented for antidromic reflex conduction has not been accepted (Hinsey, '28; Hinsey and Gasser, '30). The literature concerning an inhibitory action on sweat secretion mediated by the dorsal roots is considered by Müller ('29).

If there is any efferent conduction over the dorsal roots, it must be subserved in one of two ways. The ordinary sensory fibers may conduct antidromically with reversal of the polarity of the synapse in the central gray matter (Kohnstamm, '00). On the other hand, fibers may arise in the spinal cord and pass either to a synaptic junction in the dorsal root ganglion or directly through the ganglion to reach the site of their physiologic action. It is with these fibers of intraspinal origin that we are concerned in this review.

The difference in results from similar experimental procedures upon this problem is merely an expression of the many pitfalls which await the experimental neurologist, who oftentimes fails to recognize the fact that the methods at his disposal are not as infallible as he may deem them to be. A consideration of the phylogeny and ontogeny of the nervous system is extremely valuable in the interpretation of experimental methods. For this reason, it has been thought worth while to consider the fiber content of the dorsal roots from a comparative point of view. While a complete treatment is beyond the bounds of this communication, an endeavor will be made to give a summary of some of the important contributions. A detailed account is given by Kappers ('20). In considering the content of the dorsal roots of the different vertebrates, it is important to remember that there may be present afferent fibers (both somatic and visceral) with cells of origin in the dorsal root ganglia, afferent fibers with cells of origin within the spinal cord, and visceral efferent and somatic efferent ones of intramedullary origin.

THE LOWER VERTEBRATES

In *Amphioxus*, a part of the sensory ganglion cells is found within the spinal cord in the hypothetical primitive position for vertebrates; while most of them have progressed somewhat toward the periphery and are found scattered along the

dorsal root even beyond its division into dorsal and ventral rami (Johnston, '05). Although the latter are not grouped into an extramedullary spinal ganglion, they may be thought to occupy a position which is typical for the higher vertebrates. Visceromotor fibers traverse the dorsal roots instead of the ventral ones, which are made up of somatic motor fibers.

An extramedullary spinal ganglion is present in *Petromyzon*. Intramedullary sensory ganglion cells have been denied by Tretjakoff ('09), but they are said to be present by Kolmer ('05) and Beccari ('09). The majority of the visceromotor fibers course in the dorsal roots and it is possible that a few may be present in the ventral ones.

The dorsal and ventral roots join in the Elasmobranchs and course in mixed nerves in contrast to the failure of union of these roots seen in *Amphioxus* and *Petromyzon*. In the adults, all sensory cells are located in an extramedullary spinal ganglion. The embryos, however, possess intramedullary sensory cells found in the dorsal median portion of the spinal cord. These are found only in larval stages and send peripheral branches to the skin and to skeletal muscle. Their development, structure and disappearance were described by Beard ('92, '96). Just as in the Amphibia, these Rohon ('84)—Beard cells disappear during larval life; they do not move out to the spinal ganglia. The visceromotor fibers course through the posterior roots. It is not definitely known whether or not some of these visceral efferent fibers make their exit from the spinal cord over the ventral roots.

In the bony fishes, the sensory fibers have their cells of origin in extramedullary spinal ganglia as well as from cells within and above the spinal cord. These intra- and supramedullary sensory ganglion cells are present not only in the larvae but persist in the adult forms (Kappers, '20, p. 138). Visceral efferent fibers pass out over both the dorsal and ventral roots.

AMPHIBIANS AND REPTILES

Considerable work has been done on the anatomy and physiology of the dorsal roots in the Amphibia. In the larval stages Rohon-Beard cells are present. Fundamental studies have been made upon them in the correlation of their structure and function by Coghill ('14, '29) and by Herrick and Coghill ('15). However, in the adult forms these intramedullary sensory cells have disappeared and extramedullary spinal ganglia are present. The ventral roots contain somatic motor and visceral motor fibers. Steinach and Wiener ('95) and Steinach ('98) believed there were dorsal root motor fibers for the oesophagus, stomach, rectum and bladder. Horton-Smith ('97) was unable to confirm this for the viscera, but he did find somatic motor fibers in the dorsal roots in a limited number of cases. In seven of twelve hundred dorsal roots, Wana ('98) found somatic motor fibers to the skeletal muscles of the hind limb in the frog. Dale ('02) obtained contraction of certain skeletal muscles in three of twelve cases with *Rana temporaria* but there was no trace of this effect in ten experiments upon the toad. He did not elicit any visceromotor effects from the 6–7–8–9–10 dorsal roots. He sectioned these roots between the ganglia and the cord and allowed seventeen, thirty, thirty-seven, and forty-nine days degeneration. In the peripheral cut ends, he did not find a single fiber showing any sign of degeneration. In the proximal stumps of the dorsal roots, the myelinated fibers followed the Wallerian law of degeneration; furthermore, methylene blue preparations failed to reveal any unmyelinated fibers of intraspinal origin in these

proximal stumps. After an investigation of the autonomic system in the frog, Langley and Orbeli ('10) believed that the presence of visceral efferent fibers in the posterior roots was a rare phenomenon and not a normal distribution. Elze ('23), after section of the dorsal roots in frogs and toads, saw degenerating fibers in the peripheral stump and intact ones in the central portion of the roots.

In adult reptiles, the sensory ganglion cells for the spinal nerves are located in the dorsal root ganglia. The ventral roots contain somatic motor and visceromotor fibers. It cannot be said with certainty whether or not a few visceral efferent fibers course in the dorsal roots. In the cervical segments of lizard embryos, Beccari ('14) found cells in the medial portion of the ventral horn whose fibers passed out to join the dorsal roots by way of separate filaments of exit, slightly ventral to the dorsal roots proper. These cells are typical motor cells and resemble the somatic motor cells in the anterior horn. The peripheral destination of these fibers has not been shown, any more than that they join with fibers of the dorsal roots. Banchi ('03) saw these cells in the cervical cord of the turtle. Van Gehuchten ('96) failed to find them in the embryos of the snake *Tropidonotus natrix*. His observations confirmed those of Retzius ('94).

BIRDS

The afferent fibers all arise from extramedullary dorsal root ganglia in the spinal nerves of birds. The visceral and somatic efferent fibers leave the cord by way of the ventral roots. However, motor posterior root fibers have been described in the spinal cord of chick embryos. These posterior radicular cells of von Lenhossék are situated in the medial and lateral portions of the anterior horn and are said by Kappers ('20) to be present only in the cervical segments. The axones pass dorsally to make their exit in the posterior roots and they have not been traced beyond the ganglion. These have been described by von Lenhossék ('90) in chick embryos of four and five days incubation, by Cajal in those of five and six days ('90) and fifty-six hours ('08), by Van Gehuchten ('93) in those of eleven days, by Martin ('95) in twelve day embryos and by Tello ('22) in three and four day embryos. They are large multipolar cells resembling somatic motor ones. Their functional interpretation has never been made with certainty. Although the majority of the visceral efferent fibers leave the spinal cord by way of the ventral roots, perhaps these posterior root motor fibers should be considered as visceral efferent. Their situation in the cervical cord of reptiles and birds led Beccari ('14) to suppose that they are the forerunners of the spinal accessory nerve. In grown mammals where the spinal accessory is derived from the cervical segments, they are found in the accessory rootlets instead of in the dorsal roots. Thus they may represent somatic motor fibers which pass out over the dorsal roots instead of over the customary path in the ventral ones. Proof is certainly not present that these fibers are anything else than motor fibers to skeletal muscle. However, in the absence of definite evidence to the contrary, it must be admitted that there may be visceral efferent fibers in the dorsal roots not only in the cervical segments but in other portions of the spinal cord of birds.

MAMMALS

In the spinal nerves of mammals, the sensory fibers, both somatic and visceral, have their cells of origin in the dorsal root ganglia. The somatic and visceral efferent fibers, with cells of origin in the central gray, course in the ventral roots.

Exceptions to this fundamental type of architecture are found in the cranial nerves where some of the sensory cells of origin are found within the brain stem, i.e. the nucleus of the mesencephalic root of the trigeminal nerve. Numerous experiments have seemed to indicate that there are to be found fibers with cells of origin within the spinal gray passing out over the dorsal roots of spinal nerves.

In some of Waller's ('52) early experiments on the second cervical dorsal roots, he found that a very few normal looking fibers remained among the degenerating ones ten to fifteen days after section of the dorsal root between the ganglion and the cord. In other animals, he performed the important experiment of sectioning the 2 C dorsal root on one side and removing the spinal ganglion on the other. Two months later, he observed that all of the fibers in the proximal stumps on both sides were degenerated. In unstained preparations, he saw regenerating fibers which he recognized as such both on the side where the ganglion was present and on the side where it had been extirpated. While Waller is known for the law of degeneration, some of his observations on unstained material with degeneration methods were remarkably accurate.

The work of Joseph ('87), which was at first controverted and then later confirmed by Singer and Münzer ('95), showed that, following section of the dorsal roots, degenerating fibers were seen in the peripheral stump and intact ones in the central stump of the cat. Mott ('90) sectioned dorsal roots in two monkeys and allowed thirty days degeneration time. He says, "In the lower lumbar and upper sacral segments corresponding to the roots divided, there is complete degeneration of all fibres entering the posterior horn." Sherrington ('94) found minute myelinated fibers in the proximal stumps of the dorsal roots in the lumbosacral region of the cat, five weeks after excision of the ganglia and section of both the dorsal and ventral roots. In the course of the second and third weeks, he was unable to find them. He considered the possibility that these were regenerating fibers, but inasmuch as the sensory ganglia had been excised, he did not know where to look for their origin. He did not consider the possibility that they had regenerated from the proximal stumps of the ventral roots. In a later paper ('97), he extended this work on both the cat and monkey to the segments of the spinal cord giving rise to the thoracolumbar visceral efferent fibers. He concluded that none of the fibers in the dorsal root arise in intraspinal nerve cells. Due to the fact that his method was of such nature that he observed and measured myelinated fibers of diameters from 1 to 3.5μ, it is certain that he would have seen the smallest of them. While Kölliker ('96) was able to confirm the presence of dorsal root efferent fibers in the chick embryo, a thorough search failed to reveal any such fibers in mammals including man. Similar conclusions were reached from experimental procedures by Gabri ('96, in the lumbosacral region of the dog), Van Gehuchten ('00, lumbar region of the dog), Bikeles ('03, dog), Kopczynski ('06, cervical and upper thoracic regions of the monkey), and Lapinsky ('07, dog).

On the other hand, Morat and Bonne ('97) thought they had evidence for the presence of efferent vasomotor fibers in the 6-7 L and 1 S dorsal roots of the dog. They sectioned the dorsal roots proximal to the ganglion, allowed various intervals from eight to 106 days, and stained with osmic acid. Lugaro ('06) found a certain number of unmyelinated centrifugal fibers in the posterior roots, three months or more after section and removal of the

ganglia in the dog. In preparations stained with the Cajal method, he recognized the presence of regenerating fibers, but he thought that, in addition to the regenerating fibers, there were also some efferent ones. Timasheff ('11) cut lumbar dorsal roots in dogs. Following three to fifteen days' degeneration, he examined the distal portion of the roots and their attachment to the spinal ganglia in preparations stained with the Marchi as well as other methods. About five per cent of the fibers underwent degeneration. The gray matter of the same, and to some extent that of the opposite, side in the corresponding segments showed chromatolysis in some of the cells in the anterior and lateral portions of the ventral horns.

In the course of experiments on the tract of Lissauer and the dorsal roots, Ranson ('14) made some observations on the proximal stumps of ligated and cut dorsal roots without removal of the ganglia in the lumbosacral region of the cat. These observations were reviewed by Ranson ('29). His preparations were stained with Pal-Weigert, Marchi, and pyridine silver. He says, "In none of these have I ever seen any clear-cut evidence of efferent dorsal root fibers." He is of the opinion that the unmyelinated fibers which he found in the degenerated roots can be explained only on the basis of regeneration, but he feels that the possibility could not be excluded that the fine fibers seen entering the cord may have had their cells of origin in the cord.

After excision of the dorsal root ganglia in the lumbosacral region of dogs, Nevin ('30) stained the proximal and distal portions of the roots with osmic acid and pyridine silver. His observations were negative as to the presence of efferent fibers in the dorsal roots. Tower ('31) excised the dorsal root ganglia supplying the brachial plexus in cats. After six months to a year, unmyelinated and small myelinated fibers were present in the proximal stumps. These were shown to be regenerating fibers from the ventral roots. Their entry into the posterior horn of the cord was atypical and unlike the normal distribution. Her observations supported the conclusion that there were no fibers of intraspinal origin in the dorsal roots.

Kuré ('31) has brought together the observations which he and his co-workers ('28, '30) have made on this subject. After thirteen to 103 days, many fine myelinated as well as some larger fibers (Weigert method) were found in the central stumps of divided roots in dogs. They believe that as many as forty per cent of the fibers in the dorsal root may have an intraspinal origin in the posterior gray matter. These "spinal parasympathetic fibers" are said to pass out over the dorsal roots to terminate in the spinal ganglia. The presence of chromatolysis in the gray matter of the posterior horn following dorsal root section convinced them that the cells of origin were to be found here. This chromatolysis might have been due to anemia inasmuch as section of the posterior roots also severs the blood vessels accompanying them. The spinal ganglia were not excised and the probability of regeneration was certainly not removed by the methods they employed. Furthermore, in the shorter degeneration intervals they used, incomplete degeneration must be considéred. In failing to study the entrance of the roots into the spinal cord in properly stained material instead of the cross sections of the proximal stumps, they have fallen short of the proof required for the establishment of the intraspinal origin of the fibers they describe. Gagel ('30) confirmed Kuré in eight cases in which Foerster sectioned human sensory roots

for therapeutic reasons. Although Gagel studied some sections at the root entrance zone, he did not trace the fibers into the spinal cord. Regeneration could not be ruled out in his cases. Recently Okelberry ('32) has stated that there is a considerable number of large and medium sized as well as small fibers of an efferent nature in the dorsal roots of the lumbar region in dogs.

O'Leary, Heinbecker and Bishop ('32) found regenerating fibers in pyridine silver preparations of the central stumps of dorsal roots 20 to 25 days after section and crushing proximal to the dorsal root ganglion in the cat. However when the dorsal root ganglia were removed in three successive segments and adequate degeneration time was allowed, evidence of the occurrence of intact fibers, either myelinated or unmyelinated, was lacking. They concluded that both the small myelinated and unmyelinated fibers of the dorsal roots have their cells of origin in the dorsal root ganglia.

Hinsey ('31 and '33) has presented experimental evidence that negates the occurrence of dorsal root efferent fibers in the cervical, lower thoracic and upper lumbar, and the lumbosacral segments of the cat. This is based upon absence of peripheral degeneration as shown by the Marchi method following section of the dorsal roots proximal to the ganglia and upon the absence of axones in the proximal stumps and at the root entrance zone (pyridine silver method) following removal of the sensory ganglia. Attention was called to the errors of interpretation which may result from incomplete degeneration at the root entrance zone and from regeneration even after removal of the ganglia (Cajal, 1928).

There is no indication from comparative neurological studies which would point definitely to cells of intraspinal origin in the dorsal roots of mammals, either of an afferent or visceral efferent character. There is no conclusive proof of an experimental nature which will withstand critical examination. The work of Windle ('32), based upon an examination of serial sections of early cat embryos, demonstrates the absence of such fibers in mammalian ontogeny. That Sherrington has not deviated from his original view-point is shown by the following statement, "There is no convincing evidence that in mammals the dorsal spinal roots contain any fibres having their cells of origin elsewhere than in the root ganglion; that is, the dorsal roots contain no fibres arising within the central nervous system." (Creed, Denny-Brown, Eccles, Liddell and Sherrington, '32.) As far as the morphological evidence goes, the law of the roots still seems to be valid when it is applied to the dorsal roots of mammalian spinal nerves.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE MEANING OF ANIMAL COLOUR AND ADORNMENT. *Being a New Explanation of the Colours, Adornments and Courtships of Animals, Their Songs, Moults, Extravagant Weapons, the Differences Between Their Sexes, the Manner of Formation of Their Geographical Varieties, and Other Allied Problems.*

By R. W. G. Hingston. Longmans, Green and Co., New York. \$6.00. $5\frac{3}{8}$ x $8\frac{7}{8}$; 411; 1933.

Major Hingston, a distinguished naturalist whose earlier books have been reviewed in these columns, presents to his readers an extensive array of facts concerning color and adornment in animals to support his *color-conflict* theory. This theory is that animals, broadly speaking, possess two dominating emotions, fear and anger,

> balanced, as it were, against one another. These emotions are represented on their exteriors by two opposing patterns of colour, one concealing and the other threatening. If at any moment fear predominates, then the concealing pattern will predominate in the colour-scheme and the animal will blend more closely with its environment. If, on the other hand, anger predominates, then the threatening element will predominate in the pattern and the animal will appear less like its environment.

As a concrete illustration the author uses the lion, whose tawny coat harmonizes well with the khaki plains on which it lives. When angered the lion brings his intimidating machinery into action. He spreads his mane, throwing an area of black around his head and neck; he throws his tail (at the end of which is a brush of blackish hairs) above his back and draws back and rotates his ears, bringing dark patches directly forward. The intensity of his emotions is indicated by the degree in which he renders his threatening colors conspicuous to his foe. Extending this theory to many types of mammals and lower animals, the author finds that it applies in the explanation of courtship, songs, extravagant weapons, the formation of geographical varieties and allied problems. Major Hingston's philosophical ideas concerning the meaning of color merit the careful attention of biologists.

The book contains much about the habits of animals that will be of interest to the general reader. It is well illustrated with drawings by the author, and is indexed.

VERTEBRATE PALEONTOLOGY.

By Alfred S. Romer. University of Chicago Press, Chicago. \$5.00. $6\frac{3}{4}$ x $9\frac{1}{4}$; vii + 491; 1933.

A useful reference book for biological laboratories and an excellent textbook for paleontological courses. The material is arranged as a group-by-group treatment of the vertebrates, the various ramifications of the family tree being traced out. Major structural features of each group are described in considerable detail. The work concludes with a synoptic classification of vertebrates, a bibliography of 314 titles and brief historical notes, and an index. There are 359 figures in the text.

GENETICS

INHERITED ABNORMALITIES OF THE SKIN AND ITS APPENDAGES.

By E. A. Cockayne. Oxford University Press, New York. $8.00. $5\frac{1}{2} \times 8\frac{5}{8}$; x + 394; 1933.

This book will be of great usefulness to those dermatologists who are interested in following up the genetics of skin abnormalities which come under their observation. An introductory chapter deals clearly and concisely with Mendelian inheritance. In the fourteen chapters following, widely diverse disorders are discussed, many of which are not primarily defects of the skin and its appendages but are obvious in the ectodermal structure. The work should lead to a wider interest in the recording of pedigrees and reports of families in which such defects are inherited. Geneticists will find many suggestions in the data given for profitable future lines of work. Many diagrams and tables are included in the text. The documentation and indexing are excellent.

DAS PERSÖNLICHE TEMPO. *Eine erbbiologische Untersuchung. Sammlung psychiatrischer und neurologischer Einzeldarstellungen, Band IV.*

By Ida Frischeisen-Köhler. Georg Thieme, Leipzig. 5.50 marks. $6\frac{3}{4} \times 10$; 63; 1933 (paper).

An individual has a fairly definite rhythm of tapping with a finger on a table or of patting on the floor with his foot, and there are clearly marked individual preferences for certain metronome rhythms. These tempos are so constant that they may be used as genetic characteristics, we are told; they are alleged not to vary in different age groups or in different social classes. Women go in for slightly faster rhythms than men. Identical twins show less variation in tempo than fraternal twins.

MULTIPLE SKLEROSE UND ERBANLAGE.

By Friedrich Curtius. Georg Thieme, Leipzig. 18 marks (paper); 20 marks (cloth). $6\frac{3}{4} \times 10$; 215; 1933.

A noteworthy contribution to the literature on the constitutional factor in multiple sclerosis. Many case histories and pedigree charts are given, including data on the age of onset of various symptoms in the members of each family suffering from this disease. Suggestions are made for further study of etiological factors in this malady. The book is provided with a bibliography of eleven pages, but has no index.

GENERAL BIOLOGY

SÉNILITÉ ET RAJEUNISSEMENT.

By Auguste Lumière, J. -B. Baillière et Fils, Paris. 18 francs. $5\frac{3}{8} \times 8\frac{1}{4}$; 160; 1932 (paper).

In the earlier chapters of this book the author gives a short treatment of his thesis elaborated fully in his *La Vie, La Maladie et La Mort*, noticed in Volume 4 of this REVIEW, namely, that the colloidal state is a necessary condition of life, and that sickness and death result from the destruction of this state. In the chapters on senility he advances his theory that senescence results from the evolution of the colloids and micelloids toward destruction by precipitation or flocculation. Theoretically this destruction should begin at the same age in all individuals of the same species, but infinitely variable external factors may, and do, hasten the destruction. In this connection he moralizes a little in the *modicus cibi, medicus sibi* vein. The last chapter contains a review of the work of Steinach, Voronoff, and others on rejuvenescence from which the author concludes that:

> In reality, the old colloids are not modified by means of extracts of genital glands, but these latter produce an excitation of the cells which provokes their multiplication. It causes new cells and consequently new colloids and micelloids which are the cause of the phenomenon of rejuvenescence, more or less appreciable and always temporary.

A bibliography is provided.

URZEUGUNG UND LEBENSKRAFT. *Zur Geschichte dieser Probleme von den ältesten Zeiten an bis zu den Anfängen des 20. Jahrhunderts.*

By Edmund O. von Lippmann. Julius Springer, Berlin. 9.60 marks. $6\frac{3}{8} \times 9\frac{1}{2}$; viii + 135; 1933 (paper).

The eminent historian of chemistry relates to us the history of the problem of the origin of organisms, from the earliest times down to the beginning of the twentieth century. The problem is one that has always busied and baffled the human mind, and the record of the various hypotheses proposed for its solution shows the same conflict between mechanism and vitalism ever emerging during the course of the centuries, though under different forms or names and remaining in part unchanged in our own times. The author reaches the conclusion that the problem of the nature and origin of life cannot be solved on the basis of natural science alone but belongs ultimately to metaphysics. The story is told in a manner that will appeal not only to scientists, physicians, and philosophers, but to the educated in general as well. No *Fachkenntnis* is required.

Three indices—names of authors and anonymous works; geographical and proper names; topical index—give the book a special value as a work of reference.

MODERN THEORIES OF DEVELOPMENT. *An Introduction to Theoretical Biology.*
By Ludwig von Bertalanffy. Translated and adapted by J. H. Woodger. Oxford University Press, New York. \$2.50. 5 x $7\frac{1}{2}$; x + 204; 1933.

Professor Woodger has done an excellent piece of work in the translation and adaptation for English readers of this important contribution to the philosophy of biology. To the original German edition have been added the results of such investigations as have appeared since its publication. The book is not a summary of investigations on the physiology of development, but is an attempt to show "a way to a new organization of biology which, we believe, will permit the present difficulties and contradictions—or at least many of them—to be overcome." The principal current theories are described and critically evaluated. Those experimental results which are most essential from the theoretical standpoint are described. The translating has been done with great skill. There is a bibliography and an author and subject index.

THE LAMARCK MANUSCRIPTS AT HARVARD.
Edited by William M. Wheeler and Thomas Barbour. Harvard University Press, Cambridge. \$2.50. $5\frac{1}{4}$ x $7\frac{7}{8}$; xxxi + 202; 1933.

The Museum of Comparative Zoölogy at Harvard University possesses six Lamarck manuscripts. In this volume transcriptions of the original French texts are given together with their English translations. The first is on phrenology. Lamarck discusses Gall's theory that "our higher faculties and persistent inclinations give rise to external signs consisting in more or less conspicuous prominences of the brain case." This manuscript and the one which follows on Idea and Imagination are of considerable length. The other four, which are much briefer, are as follows: Analytical revision of human knowledge, Zoölogical questions (with drawings), Natural history, and a Report on observations made on a botanical excursion.

In an introduction the editors give a general account of the manuscripts and a comparative characterization by Crookshank of Lamarck and Darwin. As would be expected the editing is done with scholarly insight and skill throughout.

EDUCATIONAL BIOLOGY. *Second Edition.*
By William H. Atwood and Elwood D. Heiss. P. Blakiston's Son and Co., Philadelphia. \$2.75. 6 x $8\frac{3}{4}$; xiii + 475; 1933.

To those who are interested in the teaching of teachers of biology and who favorably received the first edition of this work, this, the second edition, will no doubt continue to be useful. In somewhat less than 500 pages, including 269 illustrations, the reader moves rapidly from centrosome to *Sequoia sempervirens*, from instinct to acquired immunity. Obviously, only the simplest and most superficial discussions can be given. Each chapter or unit is followed by a list of questions, presumably to stimulate the student to further reading, and by a short bibliography. For the most part the references are general textbooks, many of which are repeated in successive lists, and it may be doubted

that such entries as "Bulletins of the various states' Departments of Agriculture" and "Wright, *Frogs*, U. S. Bureau of Fisheries" will arouse the naive student to independent reading or introduce him to acceptable bibliographic notation.

Old Age Deferred. *The Prevention of the Disabilities and Diseases of Old Age.*
By Bernard Hollander. Watts and Co., London. 3s. 6d. net. $4\frac{3}{4} \times 7\frac{1}{4}$; ix + 102; 1933.

This little book written by an English physician who aims to reassure those who see old age on the horizon, contains much sound information and wise advice. It begins with the question "What is old age?" and proceeds through such topics as the physical signs of senility and the mental changes which occur, the average duration of life, the chemistry of life, the chemistry of the body and preservation of virility, to general rules for a comfortable attainment of advanced years. In the section on "One of nature's remedies for premature senility" the author discusses a phase of the subject which has received far more attention in Europe than in the United States, namely, the rejuvenating powers of the waters of natural springs. The work concludes with a short list of references and a detailed index.

Medical Biology. *A Laboratory Manual of Bacteriology, Mycology, Immunology, and Parasitology; Consisting of Experimental Guide, Interpretive Text, Atlas and Protocol Form.*
By William B. Sharp. University of Texas, Galveston (William B. Sharp). \$4.50. $6\frac{1}{8} \times 9$; iv + 443; 1933 (paper).

A laboratory handbook of bacteriology, mycology, immunology and parasitology. It is designed to aid the student in the organization, interpretation and systematic recording of data he gathers in the laboratory. The seven parts of the manual are as follows: General bacteriology, sanitary bacteriology, milk and meat product sanitation, contamination of foods and drinking water, clinical bacteriology and medical zoölogy. Each part is divided into sections which give general discussions of the main points in a particular field, illustrations and important exercises with space for notes and records which the student may wish to record. Altogether the work contains over 100 figures. It is indexed.

The Great Enigma. *A New View on the Outlook of Life.*
By Hugo H. Schauinsland. Translated from the German by Walter H. Schauinsland. E. P. Dutton and Co., New York. \$1.25. $5\frac{1}{4} \times 7\frac{1}{2}$; 93; 1933.

The enigma of life is how to account for the development of complete organisms, and while Dr. Schauinsland is gracious enough to concede that science has made some slight progress in describing the changes that go on in living matter he is quite firm in saying that scientific methods can never account for correlation and coordination of the parts of an organism. For this one must invoke spiritual forces; vitalism will not do because it is not potent enough. It takes real, old-fashioned, religion to explain biology. Schauinsland is so sure he is right that it is not necessary for him to argue his points, he merely tells you what is right and what is wrong. This method has one merit, certainly: it wastes little paper.

A Textbook of General Biology.
By E. Grace White. The C. V. Mosby Co., St. Louis. \$3.00. $5\frac{1}{2} \times 8\frac{1}{2}$; 615; 1933.

An attempt has been made to write a sort of minor treatise on biology constructed on formal lines, which would give "the beginner a glimpse into all phases of biology," and so conscientiously has this plan been followed that almost every biological theory, even the newer and still dubious ones, is referred to somewhere. The treatment is uneven, as a result, and a good many parts suffer from lack of clarity of expression. There is a long glossary in the back of the book, in which numerous terms are badly defined, and a good index.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 407. Rotationsdispersion.*

By Marie Wreschner. Urban und Schwarzenberg, Berlin. 4.50 marks. 7 x 10; 92; 1933 (paper).

A brief discussion is provided of the theory and methods of polarimetric measurement with monochromatic light in the visible spectrum and also in the infra-red and ultra-violet.

HUMAN BIOLOGY

LINCOLN. *A Psycho-Biography.*

By L. Pierce Clark. Charles Scribner's Sons, New York. $3.50. 6 x 9; xv + 570; 1933.

LINCOLN AND THE DOCTORS. *A Medical Narrative of the Life of Abraham Lincoln.*

By Milton H. Shutes. The Pioneer Press, New York. $5.00. $5\frac{1}{2}$ x 9; 152; 1933.

These two volumes are welcome additions to the mass of Lincolniana, particularly to the human biologist. Lincoln is one of the great type specimens of *Homo sapiens*, worthy always of more penetrating study. Somewhat belatedly it has now come to be generally accepted that in order to get any real understanding of a man's life it is necessary to know everything possible about his physical and mental well-being (or alternately ill-being). These books before us are definite and significant contributions to such knowledge about Abraham Lincoln.

Clark's treatise is, by a great deal, the more important. A careful reading of it has convinced us that it gives for the first time a really sound, trustworthy and comprehensive picture of the personality of the man. It is not news that Lincoln was a psychoneurotic. But we have not hitherto had such a clear and cogent analysis of just how and why he was such. It is obviously impossible to summarize in a paragraph of a review 570 pages of close reasoning about a complex personality. But some idea, at least, of the author's conclusions may be got from the following:

We therefore see in the Lincoln character two violently opposing forces, intellectual and emotional. The one embracing his keen interest, his logical process of thought, his enduring grasp upon reality and his sane judgment, through which he would become a free thinker in the best sense of the term, but on the other hand we find as deeply implanted the maternal identification, the deepest emotional need of continued protective support against a loveless existence. Thus the helplessness and its needfulness are born out of the identification with the mother-image, an emotional fixation in which the need of love is overwhelming. In Lincoln we have his identification with the father by which he takes over the father's masculine strength; he places it, however, to the father-surrogate's undoing in the field of religious thought, but a still deeper implant of dependency will not let him off, for the longing for security and support from the all-giving mother is also present. No wonder the various contemporaries who happen to view but a facet, one side of Lincoln's mind formations, interpret so differently his religious life. Lincoln personifies the travail of all who would give up the longing to return to the mother's loving arms, to re-experience the Nirvana of the prenatal existence. It is indeed a Sisyphus' task for the life forces to strive to overpower the death impulses, yet for life's span Lincoln valiantly strives to ward off the death impulses, and never does he succumb completely to religious domination. He takes as his mentor the totality of the ingredients of the mind, the conscience, as his omnipresent Thou shalt and Thou shalt not.

Unfortunately Dr. Clark writes like a psychiatrist. Why it is that the modern psychiatrist, with few exceptions, feels compelled in his writing to be at once so tediously verbose and so tortuously precious, has never been made clear. To say of the evening gatherings of lawyers and judges in a dingy hotel room for a shot of whiskey before going to bed after a busy day on the circuit in the middle west nearly a century ago that "in their recalescent glow one catches a strange illumination that this conviviality borders closely upon a sensuous ecstasy, a dionysiac orgy that seduces men from their homes" (p. 132) is not the sort of writing likely to win sensible readers.

Dr. Shutes' book is smaller and more matter of fact. It furthermore is not written in the irritating historical present tense. It confines itself to an account of practically all the contacts of Lincoln and his family with the medical profession, going into such details as his drug store bills, the prescription for his spectacles, etc. It forms an excellent supplement and foil to Pierce's more expansive treatise.

Both books have bibliographies and indices. Both are well worth reading.

On Ancient Central-Asian Tracks.
Brief Narrative of Three Expeditions in Innermost Asia and North-Western China.
By Sir Aurel Stein. The Macmillan Co., New York. $10.00. $6\frac{1}{2} \times 9\frac{1}{4}$; xxiv + 342; 1933.

In this book, based on a course of Lowell lectures, the distinguished author presents a succinct account of his explorations, archeological and geographical, in Chinese Turkestan and the neighboring regions. After two introductory chapters, dealing with the geography and history of central Asia, a narrative of his travels and excavations on his three expeditions of 1900 to 1901, 1906 to 1908, and 1913 to 1916, is given. Among his interesting finds in the ruined cities of the desert were frescoes and votive panels of painted wood from Buddhist shrines in a style derived from the Graeco-Buddhist art of north-west India; a panel representing Rustam, the great hero of Persian epic legend, as a Buddhist divinity; documents on wood in Kharoshthi, an ancient Indian script; and clay seals bearing the figures of Pallas Athene, Eros and Heracles. He was also able to trace the remains of the wall which the Chinese Emperors of the Han dynasty in the second century B.C. built to protect the corridor between China and the west against Hunnish raids. His discoveries thus illustrate the singular mixture of Indian, Greek and Chinese influence to which this far off region of central Asia was subjected. The most interesting of his finds, however, was a great mass of Buddhist and secular manuscripts and painted banners which had been hidden for nearly a thousand years in a rock-cut chamber of the Caves of the Thousand Buddhas. Among the discoveries here were a block printed roll dated A.D. 868, the oldest printed book yet found; Manichaean texts which throw new light on that hitherto little known religion; and the "most remarkable, comprehensive and also best preserved" manuscript of the earliest Turkish literature.

This is a fascinating book, made still more vivid by excellent illustrations, many of them in color. It contains also a map of Chinese Turkestan and the adjacent regions, an index and a bibliography of Sir Aurel Stein's writings.

Adventures of Ideas.
By Alfred N. Whitehead. The Macmillan Co., New York. $3.50. $5\frac{3}{4} \times 8\frac{1}{2}$; xii + 392; 1933.

The title of this book, Professor Whitehead explains, bears two meanings. On the one hand, the book traces the adventures of certain ideas in promoting the slow drift of mankind towards civilization; on the other hand, the book itself is the fruit of the author's adventure in framing a speculative scheme of ideas which shall be explanatory of the historical adventure.

The first adventure is in the social realm: that of Plato's idea of the essential greatness of the human soul in its effect on slavery. The classical civilization was based on slavery; Plato himself must have been a slave owner. Yet his concept working on the minds of the Stoic lawyers of the Roman Empire, of the Christians, of the sceptical humanitarians of the eighteenth century, produced first the amelioration and finally the abolition of slavery.

Part II, dealing with the influence of scientific ideas upon European culture, ends rather curiously with an appeal to the Protestant clergy for leadership in the new Reformation which is in progress. Just what the religion issuing from this new Reformation will consist of is not entirely clear to us, but there seem to be three main ingredients: (1) the Platonic doctrine that the divine element in the world is a persuasive, not a coercive element; (2) Jesus as the supreme illustration of this doctrine; (3) the doctrine of the early Christian theologians of the immanence of God in the world.

Part III deals with the more particular problems and debates of the philosophers; while Part IV treats of the five qualities that define a civilized society: Truth, Beauty, Adventure, Art, Peace. The latter refers, not to political relations, but to "a quality of mind steady in its reliance that fine action is treasured in the nature of things."

Evidently Whitehead has traveled a long distance from the *Principia Mathematica*. Yet it is perhaps significant that Russell has journeyed along much the same road. After all, man is not a disembodied intellect but a social animal, an agent faced with the necessity for making decisions

between alternative actions, and longing to find some ultimate goal towards which his actions may tend. "Life" said Samuel Butler, "is the art of drawing sufficient conclusions from insufficient premises." And if the conclusions are not always wholly sufficient, it is of the essence of adventure that it does not always reach the sought for goal.

OLD AGE AMONG THE ANCIENT GREEKS. *The Greek Portrayal of Old Age in Literature, Art, and Inscriptions, with a Study of the Duration of Life Among the Ancient Greeks on the Basis of Inscriptional Evidence.*

By Bessie E. Richardson. The Johns Hopkins Press, Baltimore. $4.00. 6 x 9; xv + 376; 1933.

This useful addition to the literature of human biology presents the results of a thorough and painstaking combing of the classics for everything that could be found relating to longevity, senescence and senility among the Greeks. The material so collected is then discussed from a variety of angles. Seven of the thirteen chapters (I, VI, VII-XI inclusive) deal with the physical aspects of senility, either as revealed by written descriptions and allusions, or by vase paintings, or by one or another form of sculpture. Of the remaining chapters II concerns itself with the mental and emotional characteristics of senility; III with the duties and interests of the aged citizen; IV with the attitude of the Greeks towards the aged; V with rejuvenation. Chapter XII lists remarkable examples of longevity, and XIII attempts, on the basis of the stated ages at death in the sepulchral inscriptions of 2022 persons, to determine the distribution of duration of life. The average age at death turns out to be 29.43 years. But there is a patent deficiency of records for deaths under 20 years. Altogether it is to be regretted that the author did not seek the advice and guidance of a competent biostatistician when preparing this chapter. She plainly lacks a clear understanding of the various technical concepts and procedures of either the statistical or the actuarial calculus.

An indication of the thoroughness of the work on the literary side is given by the first entry in the selected bibliography, which reads as follows: "A. Literature. Nearly all the Greek authors have been consulted." The documentation (in footnotes) throughout is meticulous. The illustrations are numerous and excellently reproduced. Besides a general index there is a concordance to literary passages, and a concordance and index to art, tabulating each art object used in the study.

No library or laboratory dealing with human biology can afford to be without this book.

ARCTIC VILLAGE.

By Robert Marshall. Harrison Smith and Robert Haas. $3.00. $5\frac{3}{4}$ x $8\frac{1}{2}$; xii + 399; 1933.

Here is an entertaining book of much interest and value to students of human biology in the broadest sense of the term. The author, a trained botanist and forester, first spent a summer in the village of Wiseman in the upper reaches of the Koyakuk River, well above the Arctic Circle in Alaska, and liked the place and its inhabitants so much that he went back again and stayed more than a year. The book is a penetrating description and analysis of the inhabitants as individuals and as a social group, in their relations to each other and to their environment, an environment extremely harsh and forbidding by conventional standards and attitudes.

The net upshot of the study is to demonstrate that the people of Wiseman are just as well off in terms of human happiness as people anywhere else in the world, and in some respects better off. This result will strike the average city dweller as more remarkable than it really is. To anyone who has had the good fortune to have been born and brought up in, or to have lived any considerable length of time in a remote backwoods community, some of Marshall's findings in Wiseman will seem commonplace, so much so in fact as to throw parts of the book almost into James's category of the "painstaking delineation of the obvious."

The total population of Wiseman consisted of 127 persons, of whom 77 were whites, 44 Eskimos, and 6 Indians. The

author's technique was to become intimately acquainted with these persons as individuals, test and measure them in a variety of ways, psychologically and physically, and at the same time by becoming himself wholeheartedly a constituent member of the community get a thorough understanding of the organization and interplay of social forces and relations. That Dr. Marshall is sympathetic to the sort of life he found is sufficiently indicated by the dedication of the book, in which he calls it "the happiest civilization of which I have knowledge."

The book is a contribution to human biology of real significance and importance. Its thirty-seven chapters are ordered in seven parts, dealing respectively with the background, the people, the economic life, the communal life, the sexual life, the recreational life, and Koyakuk philosophy. The illustrations are abundant and beautifully reproduced from the author's own photographs. There is an excellent analytical index.

SOME BASIC STATISTICS IN SOCIAL WORK. *Derived from Data of Family Agencies in the City of New York.*

By Philip Klein with the Collaboration of Ruth Voris. Columbia University Press, New York. $3.50. $5\frac{1}{2} \times 8\frac{1}{2}$; xiv + 218; 1933.

This study dealing with family welfare work in Manhattan and the Bronx in the City of New York was commenced before the depression era and covers two years of the depression itself. Four agencies coöperated in the work: The Association for Improving the Condition of the Poor, the Catholic Charities, the Charity Organization Society, and the Jewish Social Service Association. The investigators "attempt to formulate, for one of the most important social work activities, statistics appropriate to its task, accurate and uniform, and capable of being related to community life." The specific objectives of the inquiry growing out of this general purpose are defined in the form of a series of questions. Then follows a discussion of

the relation between economic conditions and the operations of the family agencies, the nature and inclusiveness of the organizations studied, the merits of statistical units employed in measuring their work, the possibility of obtaining accurate and uniform statistics and of distributing them by small areas, and finally the applicability of the findings of the study beyond the immediate field of family social work or the particular territory covered by our agencies.

The work includes numerous tables, graphs, and figures. In four appendices will be found notes on collecting data and on additional statistical material. There is an index. Porter R. Lee contributes a foreword.

HOLLOW FOLK.

By Mandel Sherman and Thomas R. Henry. Thomas Y. Crowell Co., New York. $2.00. $5\frac{1}{8} \times 7\frac{1}{2}$; viii + 215; 1933.

The early migrations of settlers into West Virginia and Ohio in Colonial times left small groups of people of English and Scotch-Irish ancestry stranded in the hollows and valleys of the Blue Ridge Mountains of Virginia. Their descendants are there still; if their parents happened to have settled in the lower valleys they have been involved to varying degree in the social and economic changes of the nation, but in the more inaccessible hollows are little communities of highly inbred people who have been almost completely isolated from the rest of the world for generations and who have forgotten what schools, churches, and systems of government are.

The material which forms the basis of this story of mountain people was obtained from a study made during a period of two years. Two psychologists and their assistants, a nutritionist, a psychiatrist and sociologists took part in the investigation. In addition, a field worker intimately acquainted with the mountain people lived amongst them continuously during the two years gathering social and economic data. Not only did these workers make frequent trips to the mountains to administer tests, but they also lived for varying periods in the cabins of the mountain people in order to become familiar with their habits, customs, daily routine, desires and thoughts. The names of the communities and inhabitants are fictitious.

A journalist and a psychiatrist collaborated in writing this book, and they have an interesting story to tell.

Fighting the Insects. *The Story of an Entomologist. Telling of the Life and Experiences of the Writer.*

By L. O. Howard. The Macmillan Co., New York. $2.50. $5\frac{3}{4} \times 8\frac{1}{2}$; xvii + 333; 1933.

This charming autobiography by the *doyen* of American entomologists embodies a great deal of general biological, social, and governmental history, as well as strictly entomological. Dr. Howard's manifold talents and graces combined with his long-held official position as chief entomologist of the federal government make his life an unusually interesting and varied one. He can look back over it, as he does in this book, with the satisfaction of having missed but few pleasant bets, as the phrase goes. While he is very modest about it all, his solid achievements must also be a great comfort to his declining years, for it can be quite truly and literally said of him that in his life time he changed the status of economic entomology, and brought it to a position of dignity and importance second only to medicine among the applied biological sciences.

This story of his life is most entertainingly written, chatty and digressive as an autobiography ought to be. Dr. Howard has long had a great reputation as a *raconteur*, and happily he puts into this book many of his best stories, some of them familiar to the older generation of biologists to be sure, but very much worthy of permanent record for the delectation of generations to come.

Altogether we congratulate the genial and urbane author, with deep sincerity and hearty good wishes, upon a good life pleasantly and usefully lived, and upon his delightful account of it. May God bless and preserve him for many years yet.

William Bartram. *Interpreter of the American Landscape.*

By N. Bryllion Fagin. The Johns Hopkins Press, Baltimore. $2.25. 6 x 9; ix + 229; 1933.

In the history of American natural science the name of Bartram holds an honorable place. John Bartram was a Pennsylvania farmer who established the first important botanical garden in America, helped Franklin to found the American Philosophical Society, and was regarded by Linnaeus as "the greatest natural botanist in the world." His son William spent five years in botanical explorations in the Southern colonies, which were described in his *Travels through North and South Carolina, Georgia, East and West Florida, the Cherokee Country, the Extensive Territories of the Muscogulges, or Creek Confederacy, and the Country of the Chactaws; containing an Account of the Soil and Natural Productions of those Regions, together with Observations on the Manners of the Indians.* (Philadelphia, 1791). The book was soon reprinted in England and Ireland, was translated into German, Dutch and French, and was among the chief sources from which Coleridge, Wordsworth, Chateaubriand and other writers of the Romantic school drew their ideas of the subtropical landscape and of the noble savage. In it we find the various sides of Bartram's character represented: the careful observation of the naturalist, the esthetic appreciation of Nature of the artist, the rhapsodic piety of the Quaker. Mr. Fagin gives an account of Bartram's life, his philosophy of Nature, his studies of the American Indian, his treatment of the southern landscape, and his influence on literature. There is a bibliography of twelve pages and an index. It is to be hoped that this scholarly study will aid in making a delightful book better known.

Gypsum Cave, Nevada. *Report of the Second Sessions Expedition. Southwest Museum Papers Number Eight.*

By Mark R. Harrington. Southwest Museum, Los Angeles. $2.50. $7 \times 10\frac{3}{8}$; ix + 197; 1933 (paper).

In view of the discussions that have gone on for many years concerning the inhabitation of America by very early man this investigation, demonstrating as it does that man must have been in Western United States as early as the beginning of the late paleolithic period, or around 20,000 B.C., is a most welcome contribution to the archeology of this country.

Gypsum Cave, situated in southwest Nevada, is a limestone cave of paleozoic age; it shows considerable tilting distortion and the action of heat. The cave measures 300 feet in length and divides naturally into five rooms which have been the depository for refuse and articles belonging to man and animals for many ages. Indications that the cave was inhabited by pleistocene animals were furnished most conclusively by (1) the large deposits of dung identified as belonging to the ground sloths of that period, (2) the discovery of the skull of the giant sloth *Nothrotherium shastense*, and (3) bones belonging to pleistocene species of the camel and horse. Associated with these findings are many obviously human artifacts, the most common of which were darts, painted dart-shafts, dart points, and flint articles. Although no actual skeletal remains of early man were unearthed, there can be no doubt that man inhabited the cave and met face to face animals long since extinct and definitely living in this country during the paleolithic era.

This is a contribution of first-rate importance.

Displacement of Men by Machines. *Effects of Technological Change in Commercial Printing.*

By Elizabeth F. Baker. Columbia University Press, New York. $3.50. 6 x 9; xxii + 284; 1933.

The aim of this investigation was to determine the extent to which men have been displaced by machines in the printing industry, which has been mechanized to a high degree, particularly within the last 20 years, and in which competition is unusually keen. Remarkably enough, "despite these improvements in machinery, the number of workers employed in book and job printing, instead of decreasing has steadily grown. This appears to be explained by the relatively low man-displacing power of the new machines, accompanied by an important increase in the consumption of printing." It is the unskilled assistants who are finding reëmployment increasingly difficult (there is normally a very high labor turn-over in this trade) and the human problem involved in the efforts of these men to retain their place in the industry takes up a good deal of the book. Several kinds of study are represented, and it becomes an important contribution because it appears to be one of the first attempts at a really thorough study of the labor conditions prevailing within a whole industry. It is beautifully printed and is provided with a good index.

The Story of Kalaka. *Texts, History, Legends, and Miniature Paintings of the Śvetāmbara Jain Hagiographical Work. The Kālakācāryakathā. Smithsonian Institution, Freer Gallery of Art, Oriental Studies, No. 1.*

By W. Norman Brown. Smithsonian Institution, Washington. $2.00 (paper); $2.50 (cloth). $10\frac{1}{2}$ x 14; viii + 149 + 15 plates; 1933.

Although the Jains have never been one of the more numerous of Indian sects the importance of their religious art and literature is out of proportion to their numbers. In this book Professor Brown has edited the various versions of the legend of the Jain saint Kalāka, or rather of several saints of the name who have been more or less confused with one another. In one episode of the legend, the wicked king Gardabhilla abducts the nun Sarasvatī for his harem. Kalāka thereupon conspires with the Scythians, who invade the country and make themselves rulers of it. This adventure of Kalāka in politics seems scarcely consonant with the Jain principle of doing harm to no living creature. Apparently in India as in some other countries when the principles of a religion conflict with the welfare of the church it is just too bad for the principles.

The book contains beautiful reproductions, several in color, of the miniature paintings which illustrate the manuscripts. These belong to the little known Western Indian school which preceded the Rajput and Mughal styles.

HISTORY AS A SCIENCE.

By Hugh Taylor. Methuen and Co., London. 7s. 6d. net. $5\frac{1}{2} \times 8\frac{3}{4}$; vii + 138; 1933.

Mr. Taylor's thesis is that the development of history as a science has been retarded by the circumstance that historians in general have approached their subject from the viewpoint of the moralist rather than from that of the scientist, that they have started with a prepossession in favor of freedom, or constitutionalism, or what not, and have interpreted the data to conform to their prepossession instead of deducing generalizations from an unbiassed study of the facts. However, it is easier for a writer to advocate "a passionless attitude restricted to the sole purpose of gaining knowledge" than for him to adopt it in actual practice. There is the complication that the student of human relations is himself a man and with the best will in the world to be objective finds it difficult to study them with the same detachment with which he might observe the relations of different castes of bees. In Mr. Taylor's own application of his theories to the historical phenomena of government, war and revolution we suspect from his somewhat emotional tone that his conclusions are really as much presuppositions as those of the historians whom he criticises.

THE ISLE OF AUKS.

By Nicholas Polunin. Edward Arnold and Co., London. 10s. 6d. net. $5\frac{1}{2} \times 8\frac{1}{2}$; 253; 1932.

This is a narrative of the Oxford University Expedition of 1931 up the coast of Labrador to Akpatok, an unexplored island in Hudson Strait. Many geographical and geological data were obtained, as well as information on plants and birds, polar bears and Eskimos. The latter are coming to rely more and more on the Hudson's Bay Company for sugar, flour, tea, pork and tobacco, for which they exchange their fox and seal skins. They have many stories of the Tunnits, the extinct race of giants who lived by stealing from the Eskimo hunters, until they were killed off by the Eskimo women, who used to creep up while they were asleep and drill holes in their foreheads.

Akpatok proved as forbidding as the Eskimos had reported it to be, a barren tundra bounded by almost inaccessible cliffs, swathed in fog or beaten by tempest. However, the party succeeded in establishing a camp and exploring the island, but the expedition ended in tragedy when "Polly" and "Kit" lost their way on a collecting trip and the latter died of exposure. The narrative of this trip is as graphic an account of the difficulties of Arctic travel as one might wish to find.

GOD'S CANDLELIGHTS. *An Educational Venture in Northern Rhodesia.*

By Mabel Shaw. Edinburgh House Press, London. 2s. 6d. net. $5\frac{3}{8} \times 8$; 197; 1932.

This book is based upon letters written by the authoress during a period of seventeen years in the mission school for girls which she founded under the auspices of the London Missionary Society, at Mbereshi in Northern Rhodesia, Africa. It tells

> of an attempt to conserve all that is true and good in the old life and build upon it; to link the past on to this new and baffling, and, to the Bantu, exciting present; to carry over from the old life that steadying, unifying belief in the continuity of life, its uninterrupted flow and rhythm; and so to present the Christian faith to the community and to the individual that they see it not as the white man's religion, something likely to be as useful to them as his money is, but as the fulfilment of that towards which their fathers groped; a way of life, not through foreign lands, but through the familiar ways of their own thought and belief.

The book is of value not only to those engaged in missionary work, but also to everyone interested in the education of primitive peoples. If all missionaries were like Miss Shaw their profession would be more highly respected than it is.

SOCIAL PATHOLOGY.

By John L. Gillin. The Century Co., New York. $3.75. $5\frac{7}{8} \times 8\frac{3}{4}$; ix + 612; 1933.

Social Pathology is here defined as "the study of man's failure to adjust himself and his institutions to the necessities of existence to the end that he may survive and meet fairly well the felt needs of his nature." The author believes that social pathology should be interpreted in terms

of existing sociological theories. The book is divided into five parts. Part I deals with the *Pathology of the Individual*, wherein the author discusses mental and physical ailments. Part II is a discussion of the *Pathology of Domestic Relationships*. Part III, *The Pathology of Social Organization* is a discussion of urban and rural disorganization and class and group disorganization resulting from the rapid industrialization and consequent growth of large cities. Part IV, *The Breakdown of Economic Relations*, discusses the maladjustments arising from our present economic situation. Part V, *The Pathology of Cultural Relations*, is devoted to a discussion of the changes taking place in our religious, moral, and ethical mores.

This should make an excellent textbook.

ATA KIWAN. *Unbekannte Bergvölker im tropischen Holland.*

By Ernst Vatter. Bibliographisches Institut AG, Leipzig. 18 marks. $6\frac{1}{2} \times 9\frac{1}{2}$; iv + 294; 1932.

Ata Kiwan, meaning "People of the Mountains," is the name by which the natives of the mountainous Solor-Alor Archipelago call themselves. This group of islands lies just east of Java and Bali and consists of Flores, Salor, Adonare, Lomblem, Pantar and Alor. The author of this book and his wife spent eight months on the archipelago and this account of their travels, the geography of the islands, the physique of the peoples, their culture, customs and ceremonies makes interesting reading. It is noteworthy as a record of a culture which is fast being superseded by European civilization. The natives differ from island to island not only in customs but also in physique and temperament, those of East Flores being very friendly and gentle, while those of Adonare will commit murder upon the slightest provocation. An index and a bibliography are provided.

ORIGINS OF SACRIFICE. *A Study in Comparative Religion.*

By E. O. James. John Murray, London. 10s. 6d. net. $5\frac{1}{2} \times 8\frac{5}{8}$; xvi + 314; 1933.

In this book Dr. James traces the evolution of sacrifice from its beginnings to its place in the religions of civilization. The central conception underlying the institution is, he concludes, the giving of life to promote and conserve life, to augment the power of the god and enable him to carry out his functions, to strengthen the worshipper against evil, or to set up a bond of union with the supernatural powers. With the spiritualization of the concept of Deity the primitive idea of sacrifice as a necessary condition for the continued existence of the gods has given place to the idea of free-will offerings of gratitude or of acts of atonement for wrong-doing. The evolution of sacrifice in Judaism, Christianity and the religions of the far East is traced in detail. There is a bibliography of 19 pages and an index.

THE GERMAN JEW. *His Share in Modern Culture.*

By Abraham Myerson and Isaac Goldberg. Alfred A. Knopf, New York. \$1.25. $5 \times 7\frac{3}{8}$; xxii + 161; 1933.

Dr. Myerson is professor of neurology at Tufts College Medical School and Dr. Goldberg lecturer on Hispano-American Literature at Harvard. Their book aims to present a brief summary, obviously as anti-Nazi propaganda, of what the German Jew has done in the past and is doing in the present in medicine, physics, chemistry, philosophy, mathematics, music, art, literature, journalism, drama, stage and cinema. After a short history of anti-semitism in Europe the authors give an imposing list of German Jews, with comments on their lives and contributions in these various fields. The index of names covers 9 pages.

THE HAND OF DESTINY. *The Folk-Lore and Superstitions of Everyday Life.*

By C. J. S. Thompson. Rider and Co., London. 12s. 6d. net. $5\frac{1}{2} \times 8\frac{1}{2}$; 303; 1933.

In this book about 1,500 superstitions are classified under twenty-five chapter headings such as birth, childhood, courtship, marriage, the evil eye, the hand, face, apparel, food, healing, family curses, death, bones, sailors, animals, plants,

amulets, numbers, drinking and games. The superstitions are merely described without any attempt at explanation or generalization. However, it is evident from many of them that our forefathers had a vivid, if somewhat uncritical, interest in somatology. There is an index.

THE BIOLOGICAL CONCEPT OF MAN. *A Brief Introduction.*

By A. H. Miller. A. H. Miller, Branksea Tower, Parkstone, Dorset. 2s. 6d. $5\frac{1}{2} \times 8\frac{3}{4}$; 35; 1933 (paper).

When a successful and undoubtedly busy practitioner of medicine undertakes, in 35 pages, to write a biological concept of man, it is not unreasonable to expect the work of a genius. Such good fortune is, however, not apparent in Dr. Miller's paper. As nearly as can be ascertained, the author's idea is that present day medical diagnosis, therapeutics, and medical economics can and should be revolutionized by the simple but mysterious procedure of "rejecting altogether speech as an aid to diagnosis." Reginald the Office Boy raises the question as to whether this means that in nose and throat practice the patient is not to say "Ah."

RASSENKUNDE UND RASSENGESCHICHTE DER MENSCHHEIT. *Dritte Lieferung (Bogen 19–27). Vierte Lieferung (Bogen 28–36).*

By Egon F. von Eickstedt. Ferdinand Enke, Stuttgart. 10 marks each. $7\frac{1}{8} \times 10\frac{5}{8}$; 144 each; 1933 (paper).

The first two numbers of this excellent series of anthropological and biodynamic studies of the peoples of the world were noticed in the last number of this REVIEW. The present numbers contain the conclusion of the treatment of the inhabitants of Asia (begun in *Lieferung* 2), the peoples of Europe and Africa north of the Sahara, and the negro population of Africa.

THE COCOPA. *University of California Publications in American Archaeology and Ethnology, Volume 31, No. 5.*

By E. W. Gifford. University of California Press, Berkeley, \$1.00. $6\frac{3}{4} \times 10\frac{1}{4}$; 78; 1933 (paper).

These tribes are of the Yuman family and inhabit the regions around the head of the Gulf of California. The volume is only part of a basic survey of the Yuman group, and as such consists chiefly of notes on the culture, no attempt being made at a pleasant or readable style. The author concludes that the Cocopa culture is very similar to the two great Colorado River tribes, Mohave and Yuma.

THE LAW AGAINST ABORTION. *Its Perniciousness Demonstrated and Its Repeal Demanded.*

By William J. Robinson. Eugenics Publishing Co., New York. \$2.15. $5\frac{3}{8} \times 8\frac{1}{2}$; 123; 1933.

Here are 123 pages of chatty propaganda with "case histories" written in the Robinsonian style for the physician and the layman.

ZOÖLOGY

THE HAPPY BEAST *in French Thought of the Seventeenth Century.*

By George Boas. Johns Hopkins Press, Baltimore. \$2.00. $5\frac{1}{2} \times 8$; vii + 159; 1933.

Mankind may be divided into those who admire civilization and those who do not. The former regard the process of social evolution as leading upwards; the latter look back to their pre-civilized fellows as closer to nature and therefore more virtuous than civilized man. Carrying this viewpoint one step farther some of them, for whose doctrine Professor Boas coins the word "Theriophily," find the true models of virtue and happiness in the animals. This attitude dates back to Plutarch at least, but its advocacy by Montaigne and his disciples made it a subject of considerable controversy in seventeenth century France. In reply to the objection that man's possession of reason makes him superior to the beasts some theriophiles maintained that reason is a curse not a blessing, some that the beasts also possess reason, while others seized both horns of the dilemma. But any equation of man with the other animals was felt by many to be dangerous in its moral effect. Various reverend Fathers began to beat the

drums, while Descartes set forth his famous doctrine that the beasts are merely machines. Professor Boas traces the various stages of the controversy until in the eighteenth century it was transferred from the field of theology to that of biology.

LES PHÉNOMÈNES SOCIAUX CHEZ LES ANIMAUX.

By François Picard. Armand Colin, Paris. 10.50 francs. $4\frac{1}{2} \times 6\frac{7}{8}$; 201; 1933 (paper).

Zoölogists, biologists, and sociologists interested in the study of the biology of social organisms will find much that is of value in this little brochure. The author discusses very thoroughly the social phenomena of living organisms from the lowest forms to man. He finds that sociability and society are based everywhere in the last analysis upon an instinct of reciprocal attraction or inter-attraction. He classifies these phenomena into definite types, distinguishing carefully between crowds and mere aggregations, and the truly social groups, associations, societies and biocenoses. In his final chapter dealing with human society, he takes special issue with the theory of Durkheim and his school, according to which society is regarded as having an artificial, antibiological origin, being based on arbitrary constraint, and likewise with the thesis of Fustel de Coulanges and others who derive society from the family. There is a short bibliography and a table of contents.

THE JUNGLE BEES AND WASPS OF BARRO COLORADO ISLAND. *(With Notes on Other Insects.)*

By Phil Rau. Phil Rau, Kirkwood, Mo. \$2.75. $6 \times 9\frac{1}{8}$; 324; 1933.

Much new and valuable material concerning the jungle bees and wasps of Barro Colorado Island is to be found in this book. The author writes entertainingly concerning the ecology and biology of these insects and their behavior attributes and adaptations. There is a section on the behavior of the giant carpenter bee, which, although not found in Barro Colorado, is of tropical origin. In the final section on mind as a forerunner of evolution the author compares the efficiency of evolution by natural selection of variations alone, and by natural selection plus mental and nervous direction. In an appendix are given descriptions of three new species of Polybia wasps by Dr. Joseph Bequaert. The volume is interestingly illustrated and contains an index. The book is an important contribution to the literature of general biology as well as entomology.

BRIEF BIRD BIOGRAPHIES. *A Guide to Birds Through Habitat Associations.*

By J. Fletcher Street. Grosset and Dunlap, New York. \$1.00. $7\frac{1}{2} \times 10$; 160; 1933.

The purpose of this volume is to render bird identification easy to the average individual. The birds listed are those which are commonly found east of the Mississippi valley, excluding the Southern States. One hundred and fifty species are illustrated and their outstanding traits and habits briefly described. There are textual references to 64 others. The author has adopted the unusual but practically useful method of grouping the birds according to their habitat associations. The drawings are in black and white, each species being exhibited as it appears in its customary haunts. It is believed that by this method it is possible to fix a bird more definitely in one's mind than by emphasizing (often unsatisfactorily) plumage coloring.

FISHES AND FISHING IN LOUISIANA. *Including Recipes for the Preparation of Seafoods. State of Louisiana, Department of Conservation, Bulletin No. 23.*

By James N. Gowanloch. Department of Conservation, New Orleans. Free; if mailed, 50¢ to cover postage. 6×9; 638 + folding map; 1933 (paper).

In this volume an earlier work (previously mentioned in these pages) has been revised and enlarged. It includes both the salt and fresh water fishes of Louisiana, together with a description of the appropriate method of capturing them, typical Southern ways of cooking them, and the laws of the State which govern the activities of both the angler and the commercial fisherman as concerns the Division of Fisheries.

The book is generously illustrated and well indexed. Two maps provide the reader with charts of the fishing grounds.

LES ARACHNIDES (*Scorpions, Araignées, etc.*). *Biologique Systematique. Encyclopédie Entomologique, XVI.*

By Lucien Berland. Paul Lechevalier et Fils, Paris. 150 francs (paper); 160 francs (cloth). $6\frac{1}{2}$ x 10; 485; 1932.

Although the morphology, biology, classification, and geographical distribution of all the arachnids are treated in this book, the greater part is devoted to the spiders. It is well illustrated with drawings and maps and equipped with indices—author, names of species, as well as an index of biological and anatomical terms. The bibliographies given at the ends of the chapters total over 400 titles. A useful handbook for the naturalist.

LOS VERTEBRADOS EXHIBIDOS EN LOS ZOOLÓGICOS DEL PLATA. *Memorias del Jardín Zoológico de la Plata, Rep. Argentine (1930–1931), Tome IV.*

By Carlos A. Marelli. Ministerio de Obras Públicas de la Provincia de Buenos Aires, La Plata. $7\frac{1}{4}$ x $10\frac{3}{4}$; 275 + 84 plates; 1931 (paper).

A list of mammals, birds and reptiles in the Zoological Gardens at La Plata, Argentina. Their Latin and common (Spanish) names, native habitat, and references to pictures, are given. The book is equipped with indices of Latin and Castilian names, and numerous plates, a few of which are in colors.

LEHRBUCH DER ENTOMOLOGIE.

By Hermann Weber. Gustav Fischer, Jena. 36 marks (paper); 38 marks (cloth). $6\frac{5}{8}$ x $9\frac{1}{8}$; xii + 726; 1933.

An excellent reference and textbook with very good illustrations. The first six chapters are respectively devoted to a discussion of (1) the skeletal and muscular systems, (2) the nervous system and sense organs, (3) integration of the sense organs, (4) digestion and assimilation, (5) reproduction and development, and (6) ecology. The seventh chapter gives a detailed classification.

INVERTEBRATE ZOÖLOGY.

By Robert W. Hegner. The Macmillan Co., New York. \$3.75. $5\frac{5}{8}$ x $8\frac{1}{2}$; xiii + 570; 1933.

About 400 illustrations appear in this excellent textbook designed for the second course in college zoölogy, in addition to eight plates showing the anatomy of animals to be dissected in the laboratory. In style it is very much like Hegner's widely used *College Zoology*. The text is concisely written, and is provided with short, selected bibliographies at the end of each chapter, and with a good index.

THE JACKAL (*With Notes on Other Quarry*).

By George Hurst. The Masters of Foxhounds Association of India, C. R. E.'s Office, Peshawar, N.-W.F.P. Rs. 3/7. $5\frac{3}{8}$ x $8\frac{3}{4}$; iv + 46; 1932–3 (paper).

This little book, written primarily for the sportsman in India, deals mainly with the jackal, which is a far more satisfactory quarry than the fox in that country. Many interesting notes on jackal habits are reported which the naturalist will not find elsewhere on record. In the text are a number of diagrams, illustrating methods of baiting and the huntsman's *cast*. There is no index.

LA VIE DES CRAPAUDS.

By Jean Rostand. Librairie Stock, Paris. 12 francs. $4\frac{1}{2}$ x $7\frac{1}{2}$; 224; 1933 (paper).

A highly readable story of the life of the common toad, *Bufo vulgaris*, beautifully written for the layman interested in natural science. This brochure belongs to the series *Les Livres de Nature* published under the direction of Jacques Delamain.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 411. Methoden der Tierhaltung und Tierzüchtung.* Containing following articles: *Methoden zur Untersuchung von Wasserhymenopteren,* by M. Rimsky-Korsakow; *Fang und Züchtung von Strepsipteren,* by Werner Ulrich; *Sammeln und Erforschung der Bienen- und Wespennester,* by S. I. Malyshev.

Urban und Schwarzenberg, Berlin. 7.80 marks. 7 x 10; 162; 1933.

In this number of the Abderhalden *Handbuch* are given methods for the collection and study of insects. Rimsky-Korsakow deals with the aquatic Hymenoptera and their use in morphologic, physiologic and genetic studies; Ulrich with the Strepsiptera; and Malyshev with the study of the nests of bees and wasps. Each part is furnished with a bibliography.

SURPRISES.

By Edith M. Patch and Harrison E. Howe. The Macmillan Co., New York. 84 cents. $5\frac{1}{2}$ x $7\frac{1}{4}$; xiii + 307; 1933.

THROUGH THE SEASONS.

By Edith M. Patch and Harrison E. Howe. The Macmillan Co., New York. 88 cents. $5\frac{1}{2}$ x $7\frac{1}{4}$; xiv + 331; 1933.

These two books for tiny tots are written in the same manner and for the same purpose as earlier books by the first of the authors, which have already been noticed in these pages. The books are designed for primary school use.

BOTANY

THOMAS JOHNSON. *Botanist and Royalist.*

By H. Wallis Kew and H. E. Powell. Longmans, Green and Co., London. 8s. 6d. net. $5\frac{5}{8}$ x $8\frac{5}{8}$; xi + 151; 1932.

The author's task has not been an easy one. At the time Johnson lived (the early part of the seventeenth century) there were many of the same name in England, of whom five were apothecaries. Not much is known of Thomas Johnson's personal life but all authentic records of his activities have been laboriously collected and recorded. Johnson's first publications were concerning his plant hunting expeditions, "simpling voyages" into Kent and Hampstead Heath. The *Mercurius Botanicus* (1634 and 1641), an attempt to enumerate all the known British plants, was his most important work, although his fame rests chiefly on the very excellent revision that he made of Gerard's *Herball* in 1632. The amount of labor involved to complete this edition within the allotted time of one year, and the very high standard of the work done testify to Johnson's great ability. During the Civil War in England he joined the Royalist forces, where, although publicly not pretending to valor, he undertook and performed many daring exploits. He was fatally wounded in battle in 1644. The book includes a list of the works, editions etc., by Thomas Johnson, a number of illustrations, and an index.

THE FRESH-WATER ALGAE OF THE UNITED STATES.

By Gilbert M. Smith. McGraw-Hill Book Co., New York. \$6.00. $5\frac{7}{8}$ x 9; xi + 716; 1933.

This book fills a real need in a very satisfactory manner.

> The following pages have been written with a twofold purpose: to enable the student to identify the fresh-water algae of this country; and to summarize the morphology and life histories of these algae. All genera found in this country are described in detail, and an illustration is given for one or more species of each. The general key on page 626 has been so constructed that vegetative characters are utilized as far as possible, and reproductive characters are included only where they are essential for the recognition of a genus. In the case of genera with fewer than 10 species occurring in this country, there is a very brief characterization of the different species. No attempt is made to distinguish between species of the larger genera. Except for certain of the rarer genera, known only from one or two stations, there is no mention of geographic distribution.

There is an extensive bibliography and an excellent index.

TRAITÉ DE CYTOLOGIE VÉGÉTALE.

By A. Guilliermond, G. Mangenot and L. Plantefol. E. Le François, Paris. 250 francs. $6\frac{1}{2}$ x $9\frac{7}{8}$; vi + 1195; 1933 (paper).

Compared with American and German

works on plant cytology this treatise is less exclusively limited to nuclear morphology and the relation of cytology to genetics, and includes certain aspects of cellular metabolism. It is a valuable and authoritative contribution to the subject and it should be useful to specialists in several other fields as well. Some idea of the scale on which it was executed can be gained from the sizes of the bibliography (which covers 105 pages) and of the separate indexes for authors and subjects (which amount to 50 pages). Unfortunately, however, these contain an irritating number of errors.

B. CARYOCYANEUS BEIJERINCK-DUPAIX 1930. *Étude Morphologique et Biologique. Recherches sur le mécanisme du phénomène de Charrin et Roger. (Agglutination sérique des Bactéries).*

By Andrée Dupaix. Le François, Paris. 50 francs. $6\frac{1}{2} \times 10$; xv + 350; 1933 (paper).

Mlle. Dupaix has included in this summary of the knowledge concerning the *Bacillus caryocyaneus* Beijerinck-Dupaix 1930, the results of her own experiments conducted in the laboratory of the eminent microbiologist Lasseur at Nancy. The first part of the book is devoted to the morphology and physiology of bacteria, and the physical and chemical conditions which influence the life and mutations of *B. caryocyaneus*. The second part concerns the mechanism of agglutination. Extensive bibliographies are given with each chapter. The list of "general conclusions" covers 13 pages.

THE CULTIVATED CONIFERS IN NORTH AMERICA. *Comprising the Pine Family and the Taxads.*

By L. H. Bailey. The Macmillan Co., New York. $7.50. $7 \times 9\frac{1}{2}$; ix + 404; 1933.

This book is one of two planned to succeed Bailey's "Cultivated Evergreens;" a second volume on the broad-leaved evergreens will follow later. The pine family and the taxads are treated in considerable detail taxonomically (about 1000 species and varieties are included, many of them illustrated by drawings or excellent photographs), and the recommendations of a number of horticulturists on the selection and planting of the various conifers are given, representing practical experience in several regions. The book closes with chapters on the insects and fungi that attack the conifers. There is a good index.

THE INDIAN FOREST RECORDS. *The Sutlej Deodar. Its Ecology and Timber Production. Vol. XVII, Part IV.*

By R. Maclagan Gorrie. Government of India Press, Calcutta. Rs. 3-2 or 5s. 6d. $7\frac{1}{4} \times 9\frac{3}{4}$; iii + 140 + 6 plates; 1933 (paper).

An attempt to clarify Himalayan sylviculture through a study of the relationship between the variation in the deodar as a timber producing tree and the plants associated with it. The fact that the deodar grows in climates ranging from the heavy monsoon to the extreme aridity found behind the ranges of the Himalayas, implies a similar wide variation of plants found in association with it. The volume consists chiefly of classification and descriptions of these plants.

WORLD WHEAT CROPS, 1885-1932. *New Series, with Areas and Yields, by Countries. Wheat Studies of the Food Research Institute, Vol. IX, No. 7.*

Food Research Institute, Stanford University, Calif. $1.00. $8\frac{1}{2} \times 11$; 36; 1933 (paper).

In this study are presented statistics of wheat production, acreage and yield per acre for each of 40 countries annually from 1919 to 1932 and for 39 countries from 1885 to 1918. It is found that wheat production has increased more slowly during the last half century than had previously been supposed, and that the greater part of this increase was due to increase of acreage rather than of yield per acre. A bibliography of sources of data is included.

Untersuchungen über die Mikrobiologie des Waldbodens. *Erste Untersuchungsreihe. Die elementaren Lebenserscheinungen der Mikroflora und Mikrofauna des Waldbodens.*

By D. Fehér, with articles by R. Bokor and L. Varga. Julius Springer, Berlin. 24 marks (paper). $6\frac{7}{8}$ x 10; vi + 272; 1933.

This is an extensive report on the microbial flora and fauna of the forests of Hungary and of the rôles they play in the nutritional physiology of the forests. It is principally concerned with the researches of Professor Fehér and his associates and includes not only studies on the distribution and identification of the bacteria, fungi, algae, and protozoa of the soil, but also the treatment of the chemical modifications of the soil they induce.

Principles of Plant Physiology. *Revised Edition.*

By Oran Raber. The Macmillan Co., New York. \$3.00. $5\frac{1}{2}$ x $8\frac{1}{2}$; xv + 432; 1933.

The second edition of this textbook for elementary classes has been expanded somewhat by the discussion of recent research. The sections on the chemical aspects of plant physiology are the best ones.

MORPHOLOGY

An Introduction to the Vertebrates.

By Leverett A. Adams. John Wiley and Sons, New York. \$3.50 net. $5\frac{7}{8}$ x 9; v + 414; 1933.

This introduction to vertebrate anatomy is intended for beginners in zoölogy and includes résumés at the end of each chapter, a glossary that defines even the commoner technical terms, and a large number of illustrations, many of them original. It is arranged to provide an outline of the characteristics on which the modern system of classification of the chordates is based, a general view of each of the five classes, fishes, amphibians, reptiles, birds, and mammals, and a comparative analysis of anatomical systems and specialized structures, the latter subject taking up most of the book. The text is smoothly and concisely written and the book is provided with a good index.

PHYSIOLOGY AND PATHOLOGY

Traité de Physiologie Normale et Pathologique. *Tome IX: Système Nerveux (Première Partie).*

By Th. Alajouanine, I. Bertrand, Léon Binet, G. Bohn, H. Cardot, L. Cornil, E. Couvreur, P. Gley, H. Laugier, R. Legendre, J. Lévy-Valensi, J. Lhermitte, M. Nicloux, Ch. Richet Fils, J. Verne. Published under the direction of G.-H. Roger and Léon Binet. Masson et Cie, Paris. 80 francs (paper); 100 francs (cloth). $6\frac{5}{8}$ x $9\frac{3}{4}$; xi + 566; 1933.

The first of two volumes on the nervous system appearing in this great French handbook of human physiology. As is the case in other volumes of the series which have been reviewed in these pages the chapters are by various authors. This volume treats of the neurone, Wallerian degeneration and restoration, the processes of nervous disintegration, nerves and reflexes, tropisms, sensibility and motor faculty, cerebral-cortical localizations, the physiology of central ganglia, cerebral circulation, convulsions, sleep, and anesthesia, biochemically considered. Each chapter is equipped with a bibliography.

Diseases of Old Age.

By F. Martin Lipscomb. William Wood & Co., Baltimore. \$4.50. $4\frac{3}{4}$ x $7\frac{1}{4}$; vii + 472; 1933.

An account of the more important facts about illnesses of the aged. The book is designed for clinical use entirely and treats of etiology and pathology only slightly. Although practically any disease can occur in old age, the author has included only those diseases which have a high incidence in old age or those which, although characteristic of maturity, may be conspicuously altered when they occur in the senile.

CANCER: *Is the Dog the Cause?*
By Samuel W. Cort. John Bale, Sons and Danielsson, London. 3s. 6d. net. $4\frac{7}{8}$ x $7\frac{1}{8}$; viii + 190; 1933.

Mr. Cort's argument, succinctly put, seems to be as follows: Cancer must have a cause; the dog is a filthy animal; therefore, the dog is the cause of cancer. This is not a form of syllogism known either to Aristotle or to any later logician. [I protest! My researches show that 557/632nds of all uplifters reason precisely in this manner. *Reginald. Office Boy.*] [This protest raises an interesting question: Are uplifters logicians? *Platy. Office Fish.*]

THE PHYSIOLOGICAL EFFECTS OF RADIANT ENERGY.
By Henry Laurens. Chemical Catalog Co., New York. $6.00. 6 x 9; 610; 1933.

A useful source book for the practitioner as well as the experimentalist. The author reviews in detail the more outstanding evidences of the physiological action of radiant energy. He emphasizes the great possibilities of helio- and phototherapy, the lack of knowledge at present of the real mode of action of radiant energy and its component parts, the dangers of immoderate use of radiant energy, particularly on the sick individual, and the importance of considering temperature and humidity in treatment. It is shown that, in many divisions the results of radiant experiments are either contradictory or inconclusive. The work contains numerous figures, tables and graphs, a lengthy bibliography and an author and subject index. The volume forms part of the *American Chemical Society Series of Scientific and Technologic Monographs.*

DAS INDIVIDUALISIEREN UND DIE ÜBERWINDUNG DES INDIVIDUELLEN IN DER KRANKENBEHANDLUNG. *Ärztliche Beobachtungen, Erkenntnisse und Wegweisungen.*
By Hermann Königer. Georg Thieme, Leipzig. 1.80 marks. $6\frac{1}{4}$ x $8\frac{3}{8}$; 58; 1933 (paper).

In this little brochure, addressed directly to practitioners of medicine, the author develops the thesis that in the successful treatment of patients the personal idiosyncrasies of each individual must be studied and carefully evaluated. Due consideration must be given to a vast multiplicity of highly variable factors of which the more important relate to bodily habitus, state of nutrition, physiological fluctuations, psychic characteristics, emotional reactions, and the variations of the course of disease processes. Obviously no attempt can be made to give detailed directions for the treatment of patients presenting the multiple combinations of these variables.

LEÇONS SUR L'ALIMENTATION. *Physiologie. Régimes.*
By Giovanni Lorenzini. Masson et Cie, Paris. 36 francs. $6\frac{1}{2}$ x 10; 325; 1933 (paper).

A biochemical and physiological study of metabolism and diet which should be useful to the dietitian and clinician. Following a general discussion of the metabolism of water, minerals, carbohydrates, proteins, fats and lipoids, the factor of age is treated. Diets are also prescribed for persons suffering from disorders of the various organ systems. The book lacks both index and bibliography.

GIANTS AND DWARFS. *A Study of the Anterior Lobe of the Hypophysis.*
By Palmer H. Futcher. Harvard University Press, Cambridge. $1.25. $4\frac{7}{8}$ x $7\frac{3}{4}$; 80; 1933.

This creditable little essay, an undergraduate honors thesis in science from Harvard University, is essentially a short history of the discovery and development of the endocrinology of the anterior pituitary. There is a modest and well selected bibliography of 97 titles.

BIOCHEMISTRY

The Mode of Action of Drugs on Cells. *By A. J. Clark. The Williams & Wilkins Co., Baltimore.* $6.25. $5\frac{1}{4} \times 8\frac{1}{2}$; vii + 298; 1933.

The Professor of Materia Medica in the University of Edinburgh has put on record his attempt to "try to discover what laws can be postulated regarding the combinations formed between drugs and cells," limiting himself to "picking out cases in which the evidence available seems most complete and trying to find if the phenomena can be explained by the application of the laws of physical chemistry" without making highly improbable assumptions. Clark is not content to catalogue the assumptions that experimenters make, as so many compilers of textbooks do; his guide in such matters is the stern William of Occam, and he has numerous and pertinent criticisms to make of a good deal of recent work in a number of fields of physiology and experimental pharmacology. He takes a healthy interest in figures also:

> In the case of acetyl choline acting on a heart-cell, the relative sizes of the cell and the molecule are as 10^{12} is to one. This is about the relation between a large whale and a small midge. The problem is to form some picture of cell structure that will explain the fact that a few thousand of these molecules when they unite with the cell suffice to modify its functions.

His concern is primarily with the experimental work of the last ten or twenty years and his book cannot fail to have a wholesome effect on all the biological sciences; that is to say, if the people doing experimental work will read it. There are indices and chapter bibliographies.

Lipoide und Ionen. *Eine allgemein biologische und ärztliche Studie über die physiologische Bedeutung der Zell-Lipoide.*
By Rudolf Degkwitz. Theodor Steinkopff, Dresden. 28 marks (paper); 29.20 marks (cloth). $6 \times 8\frac{3}{4}$; xvi + 323; 1933.

The author aims to present for the use of biologists and physicians (1) a summary of the action of lipoids and ions in models, cells, organs and mammals, with a minimum use of chemical, physical and mathematical discussions, and (2) a picture of the structural powers of these substances, and of the knowledge and problems of researches in biochemistry of their form and structure. The usefulness of this handbook is enhanced by author and subject indices, and bibliographic annotations.

Chemische Grundlagen der Lebensvorgänge. *Eine Einführung in biologische Lehrbücher.*
By Carl Oppenheimer. Georg Thieme, Leipzig. 22.50 marks (paper); 24.50 marks (cloth). $6\frac{3}{4} \times 9\frac{3}{4}$; vii + 298; 1933.

This survey is meant to supplement the various specialized textbooks on physiology and biochemistry in such a way that a medical student or a botanist or a chemist or an animal physiologist could survey the whole field of biochemistry with the aid of the standard texts. The subject matter is limited for the most part to the newer developments and to some of the problems that lie on the boundaries of the several fields of biology. There are an index and a small number of literature references.

Medizinische Kolloidlehre. *Lieferungen 4 and 5.*
Edited by L. Lichtwitz, Raph. Ed. Liesegang and Karl Spiro. Theodor Steinkopff, Dresden. 5 marks each. $7\frac{3}{8} \times 10\frac{3}{8}$; Lief. 4, pp. 233–304; Lief. 5, pp. 305–384, 1933 (paper).

The first three numbers of this series were noted in this Review on page 235 of the current volume. *Lieferung* 4 begins the discussions of the application of colloid research in medicine, the various organs and systems of the body being treated separately. These two numbers contain the following papers: Skin, by Franz Herrmann; The eye, by F. P. Fischer; Skeletal system, by R. Bucher; Colloid-chemical physiology and pathology of the joints, by C. Häbler; and Teeth, by Wolfgang Praeger.

ANNUAL REVIEW OF BIOCHEMISTRY. *Volume II.*

Edited by James M. Luck. Stanford University Press, Stanford University, Calif. $5.00. 6 x 8¾; vii + 564; 1933.

This is the second volume of a collection of brief, critical reviews of the progress made during the preceding year or so in each of twenty-five fields of biochemistry. Prominent American and European specialists have prepared the reviews and it is in every way an important and useful book.

THE VITAMINS IN HEALTH AND DISEASE.

By Barnett Sure. The Williams & Wilkins Co., Baltimore. $2.00. 5¼ x 8; xiv + 206; 1933.

The writer has made available to the layman much useful information concerning vitamins, the part they play in health and disease, their presence in foodstuffs, and their effect on milk secretion, infant nutrition, growth, appetite and the teeth. The work is indexed. There is a foreword by Walter H. Eddy.

SEX

THE SCIENCE OF HUMAN REPRODUCTION. *Biological Aspects of Sex.*

By H. M. Parshley. W. W. Norton and Co., New York. $3.50. 5½ x 8½; 319; 1933.

This book of 319 pages, printed on thick paper so that it looks even more substantial, has condensed between its covers a small encyclopedia of the biology of sex, with special reference wherever justified to human reproduction. Logically, chapter II, which sketches the phylogeny of sex, should come first; but "Human Sexual Dimorphism: Man and Woman," which constitutes Chapter I, sounds more attractive, especially to one first fingering the book at a bookstall. The last chapter on the biology of sex behavior likewise allows the book to finish with a bang.

Certain chapters must perforce content themselves with material gathered from studies on animals and plants, as for example, Chapter III on the Sex Cells: cell division, chromosomes, genes, sex chromosomes, gametogenesis, fertilization. It does not take long to say that man has 48 chromosomes and that the XY condition prevails. Chapter IV on the anatomy and physiology of the reproductive organs can be and is written from the human standpoint. The section is much better done than similar parts of many current books on sex.

The following chapter on menstruation, pregnancy, and the life of the embryo is likewise concise and in all essentials correct. It is a brief compendium of gynecology and obstetrics, normal and pathological. One wonders if there is not too much included in the chapter. Chapter VI on sex endocrinology strikes a very modern tone and discloses careful reading and a good digestion of the recent literature. In the limits of a short chapter statements must needs be categorical but one finds no violent misstatements. Chapter VII on sex traits in childhood and adolescence represents the dynamic phase of Chapter I, which is misplaced, as already noted. Perhaps the chapter shows as much as anything the dearth of exact knowledge about physical development in childhood and especially adolescence. In Chapter VIII the author follows Pearl in his conclusions concerning population growth. The author doubts the effectiveness of "positive" eugenics as the savior of the world, but gives arguments for eugenical sterilization. Birth control can hardly be regarded seriously as a "negative" eugenical measure, for "a procedure which involves scientific exactitude and constant foresight is not for the moronic or the feeble-minded."

In the last chapter, the biology of sex behavior, the author does the logical though exceptional thing: he draws upon the more exact observations, meagre as these are, on the sex behavior of lower animals, especially monkeys (Bingham, Zuckerman, Kempf). Some applications to human behavior are well stated and to the point.

The book is "authoritative," as might be expected from the pen of a popular teacher, convincing writer, and sound investigator (mostly in other fields than that dealt with

in this volume). In diction and style the book is far removed from the "popular" class. Its chief use will be in connection with courses in biology in colleges and universities.

SEX DETERMINATION.

By F. A. E. Crew. Methuen and Co., London. 3s. 6d. net. $4\frac{1}{4} \times 6\frac{3}{4}$; ix + 138; 1933.

In this book Crew presents briefly but adequately the work that has been done on the cytological and genetic aspects of sex-determination.

Sex, in a great many forms, including those with which most of us are acquainted, is determined at the moment of fertilization. The elements of the sex-determining mechanism, brought together by ovum and sperm in fertilization, have been revealed. It is established that in many of these forms, including man, the male is heterogametic, elaborating two kinds of sperm. Any egg elaborated by any female and fertilized by one of these two kinds will yield a male; the same or any other egg fertilized by the other kind will yield a female. In moths, birds and certain fishes, however, it is the female that is heterogametic. The evidence for these statements is presented in this book, being culled from the records of experimental breeding. Sex-linkage, non-disjunction, gynandromorphism, intersexuality and sex-reversal are discussed. The apparently conflicting evidence derived from instances of parthenogenesis is examined, and it is shown that the actual cytogenetical facts relating to parthenogenesis are in accord with those derived from cytological and genetical studies of forms in which sexual reproduction is the rule.

In a final chapter the author speculates on the evolution of the sex-determining mechanism. The value of the book is enhanced by a bibliography of 12 pages, a glossary, and author and subject indices.

KASTRATION INTERSEXUELLER SÄUGETIERE. *Acta Veterinaria Neerlandica, Tome I, Fascicule 1. Edited by Maatschappij voor Diergeneeskunde te Utrecht.*

By G. Krediet. J. van Boekhoven, Utrecht. 5.50 guilders. $6\frac{1}{4} \times 9\frac{5}{8}$; 120; 1933 (paper).

This is the inaugural number of a series of monographs on veterinary problems and related subjects. The investigations are to be carried on in the European and tropical parts of the Netherlands and the results published in English, French or German. The author of this first number describes castrations he performed on hermaphroditic pigs and goats. His conclusion is that the secondary sexual apparatus is influenced by the gonads, and that the hermaphrodite is not an animal in which male and female attributes exist side by side, the former influenced by the testicular, the latter by the ovarian, cells; but rather that it is an animal which to a certain degree stands *between* male and female and in which the secondary sexual organs and attributes are influenced by a particular kind of gonads *sui generis*. The monograph contains a bibliography of two titles, and several tables of measurements of sex organs of the animals before and after castration.

BIOMETRY

NUMEROLOGY.

By E. T. Bell. The Williams & Wilkins Co., Baltimore. $2.00. $5\frac{1}{4} \times 8$; vii + 187; 1933.

In this diverting book a mathematician at the California Institute of Technology considers the question: Is there more science in numerology than there is numerology in science? As a near neighbor of Hollywood he should be well qualified to judge of the former, while as a resident of Pasadena he should be an equally good judge of the latter. Although he leaves the verdict to the reader, one need not read very deeply between the lines to infer that Dr. Bell considers Eddington and Co. worthy disciples of Pythagoras, both as scientists and as numerologists.

In section 9 of the Appendix there is a neat trap for the unwary reader: "To take an example, is 279 prime? The square root of 279 lies between 16 and 17, since $16^2 = 256$, $17^2 = 289$. So we need try only the primes less than 16, namely 2, 3, 5, 7, 11, 13. A moment's inspection rejects 2, 5 as possible divisors of 279. Try 7; it won't work; neither will 11, 13. Thus 279 is prime."

It will be noted that Dr. Bell has not tried 3 as a divisor of 279. But $279 \div 3 =$

93. Thus 279 is *not* prime. In our experience it is well to watch these mathematicians carefully to make sure that they are not putting something over on us and this caution is especially necessary in dealing with such an impish mathematician as Dr. Bell.

SYMBOLIC LOGIC.

By Clarence I. Lewis and Cooper H. Langford. The Century Co., New York. $5.00. $5\frac{3}{4} \times 8\frac{3}{4}$; xi + 506; 1932.

In the earlier chapters of this book the authors introduce the student to symbolic logic by explaining the algebra developed by Boole and Schröder for use with a logic of classes and its extension to the logic of propositions and propositional functions. As a result of the fact that symbolic logic has in general been built up on a foundation originally designed to deal with the relations of classes, the relation of material implication is much broader than what we ordinarily understand by implication. Thus any two true propositions materially imply each other: "roses are red" implies "sugar is sweet." The authors have built up another system of symbolic logic based on a meaning of "implies" such that "*p* implies *q*" is synonymous with "*q* is deducible from *p*". From this system the customary system of material implication can be derived. Later chapters give the authors' development of the theory of propositions and the application of the logic of propositions to the theory of sets of postulates, while the last chapter deals with logical paradoxes and their bearing on logical theory. There is a bibliography of two pages and an index.

PSYCHOLOGY AND BEHAVIOR

UNIVERSITY OF KANSAS STUDIES IN PSYCHOLOGY *No. 1. Psychological Monographs, Vol. XLIV, No. 1, Whole No. 197.*

Edited by Raymond H. Wheeler. Psychological Review Co., Princeton. $3.75. $6\frac{3}{4} \times 9\frac{3}{4}$; v + 300; 1933 (paper).

The monograph contains in somewhat condensed form the results of thirteen separate studies organized about the general problem of configurational response. Altogether, the papers represent well-directed, thoughtful work in experimental psychology. Heading the list are two papers dealing with cerebral action currents of the dog's cortex. In one, Perkins concerns himself primarily with action currents under sound stimulation, while in the other Bartley maps on the cortex the gradients of electrical activity for a wide variety of stimuli. The latter, rather more emphatically than the other contributors, considers the theoretical implications of recent experimental work and vigorously attacks the concept of specific localization in the cortex. Of considerable interest is his spirited criticism of Pavlov's view of localization, which reads as follows: (p. 47)

> Such a view is sheer atomism. It begs the problem of organization and unity by assuming unity to be a mysterious synthetic product—order coming into existence by summating bits of chaos, a view as archaic as it is absurd. In his attempt to narrow down the conditions of behavior Pavlov has committed the logical fallacy of considering the limited reaction as a discrete process with no relation to the rest of the activity of the animal. The actual situation is that the stimulus-conditions *have been limited*, but, limited or not, an entire organism must respond to the stimuli. Had Pavlov been guided by a field theory instead of by an atomism, much of the ardent labor of the conditioned reflex school would have produced more fruitful and far reaching results. The significance of the "generalized reflex" and of differentiation would have been obvious to him at once, and would have led to an abandonment of the reflex theory of behavior.

Two papers are devoted to the investigation of animal behavior. Margery Cutsforth reports evidence of complex organization or insight in the responses of chicks and Brigden analyses the behavior of white rats that "were unable to choose the correct of three paths to a food goal when the stimulus-pattern was a combination of three vertical lights." Six papers have to do with experimental studies on human beings. Thus Patton, to study insightful behavior, devises a test of relative judgments between pairs of light intensities; Thomas Cutsforth, studying the relation of tactual and visual perception, adds data to support the *Gestalt* conception that the sensory field acts as a functional unit; Brigden finds that "perception involves the differentiation of a homogeneous

[visual] field in such a way that the parts emerge already unified and patterned;" Showalter discusses two aspects of learning, first, the initiation of the learning process by stimulation and, second, the organization of a definite patterned reaction toward which activity takes place; Warden, using five pairs of words for each of the categories, (1) synonyms, (2) antonyms, (3) object-attribute, (4) whole-part, (5) cause-effect, deals with the recall value of the different perceived relations; Sarvis stoutly defends the presence of rhythms in work and learning curves. The maturation of the college student is studied by Baldwin from retests of the National Council tests, and by Roberts from semester grades during the four school years. Finally, Wilcox and Morrison find that the nature of the aesthetic experience varies with intensity of illumination.

PHYLOANALYSIS. *A Study in the Group or Phyletic Method of Behaviour-Analysis.*
By William Galt. Baker and Taylor Co., New York. $1.00. $3\frac{3}{4} \times 6$; 151; 1933.

In this book a student of Trigant Burrow presents the principles and technique of group analysis. The object of these researches is to discover the causes of distortions in the feeling-life of man. In the phyloanalytic group meetings the students are free to express their attitudes towards their associates, attitudes which in every day life are hidden more or less successfully under the veil of courtesy. These attitudes the demonstrator analyzes. As a result of this experimental work it is found "that the prevailing 'normal' social structure is not basic or fundamental in nature but on the contrary represents a secondary and substitutive fabric which, like the fabrications of the neurotic, is without direct biological or organic foundations." Each of us builds up an affectively colored social image of himself. We and those who agree with us must be "right" and "good," while those who disagree with us must be "wrong" and "bad." As a picturesque illustration of this phenomenon in a supposedly normal group Mr. Galt quotes some of the futile bickerings of the United States Senate. The object of phyloanalysis is to make clear this mechanism and thus to bring back the attention from moralistic interpretation to organic reality. We wish that Mr. Galt had stated more specifically how successful the method is in effecting this change of attitude. Certainly a technique which could resolve many of the tensions and irritations of every day life would add enormously to the well being of mankind.

MATERNAL BEHAVIOUR IN THE RAT.
By Bertold P. Wiesner and Norah M. Sheard. Oliver and Boyd, Edinburgh. 12s. 6d. net. $5\frac{5}{8} \times 8\frac{3}{4}$; xi + 245; 1933.

This book deals "first with a description and analysis of the components of maternal behaviour and then with the results of an examination of the physiological factors related to them." In the study of the components of maternal behavior, which the authors describe in detail, the results are largely in accord with those of previous workers. It was found that maternal behavior could be prolonged by presenting successively young litters to the mother when her own young had outgrown the need of her care. In virgin rats, the retrieving response (one of the definite activities of maternal behavior) was incited in a considerable number when new born young were placed with them. Experiments on destruction of the mammillae, the effects of oöphorectomy and of extracts containing ovarian or gonadotropic hormones are discussed at considerable length. Pronounced maternal activities were observed in a group of animals oöphorectomized and some weeks later injected with extracts. The work includes 23 tables, a bibliography and an index.

THE FIRST TWO YEARS. *A Study of Twenty-Five Babies. Volume II. Intellectual Development.*
By Mary M. Shirley. University of Minnesota Press, Minneapolis. $3.00. $5\frac{1}{4} \times 7\frac{5}{8}$; xvi + 513; 1933.

This is the second of three volumes which present detailed accounts of the develop-

ment of twenty-five babies observed week by week in their homes from birth until the age of two years. This volume is divided into three parts: Part I describes the course of motor skills, eye coördination, speech, comprehension, and social habits for each baby; Part II gives records of the manner of conducting the observations and taking the records; and Part III "is an attempt to draw all the babies' observed behavior together into an orderly and meaningful whole." Among the conclusions reached is the following:

> Behavior development in infancy always proceeds in harmony with or in conformity to biological laws of development in that: (a) development of behavior follows an orderly sequence that is consistent from baby to baby; (b) there is continuity between human and animal infants in the development of behavior, as is shown by a marked similarity in their developmental sequences; and (c) both human and animal infants adhere to the anatomical laws of developmental direction in that postural and motor control begin headward and travel tailward.

Volume I of the study was reviewed in the QUARTERLY REVIEW OF BIOLOGY, Vol. 7, p. 106.

THE ORGANIZATION OF LEARNING AND OTHER TRAITS IN CHICKENS. *Comparative Psychology Monographs, Vol. 9, No. 4, Serial No. 44.*
By Jack W. Dunlap. Johns Hopkins Press, Baltimore. $1.00. $7\frac{3}{4}$ x 10; 55; 1933 (paper).

One hundred and nineteen chicks, highly homogeneous as to ancestry, age, vitality and physical environment, were used in these experiments. Ten variables concerned with general nervous activity, spacial relationships, speed in gross muscular activities and directional tendencies, were studied. The means, standard deviations, intercorrelations, reliability coefficients and correlations corrected for attenuation are given. The evidence presented indicates that

> the table of intercorrelations based on ten different tests each on 119 chicks cannot be satisfactorily explained by one general factor plus specific factors. . . . Four factor patterns were fitted to the data, one using eight factors, one using seven factors, one using six factors, and the last using four factors. A general factor pattern using six factors was derived from a consideration of the first three patterns mentioned above and tentative names assigned to the factors.

In two appendices are given notes on *directional tendency* and *fitting factor patterns.* The work includes 26 tables and a bibliography.

THE APE AND THE CHILD. *A Study of Environmental Influence upon Early Behavior.*
By W. N. Kellogg and L. A. Kellogg. Whittlesey House, McGraw-Hill Book Co., New York. $3.00. $5\frac{3}{4}$ x $8\frac{3}{4}$; xiv + 341; 1933.

In this book is reported a unique study of the infant chimpanzee. On June 26, 1931, Dr. and Mrs. Kellogg "adopted" into their family, as companion and playmate for their 10-months-old son, a female chimpanzee $7\frac{1}{2}$ months of age. During the following 9 months the two infants lived together under *precisely the same environmental conditions* while the Kelloggs observed, recorded and compared the normal and unhampered mental and physical development of their two young charges. Except for the slightly more rapid rate of development of the ape, the two made almost identical progress. In general, the ape surpassed the child only in agility. She learned, for example, to handle a spoon, to drink from a glass, and to open doors more dexterously than the child. Only in respect of imitation and mimicry did the boy clearly show superiority. Without entering "too deeply into the confusing by-paths of the heredity-environment controversy" the authors conservatively conclude; first, "That the heredities of the two are similar enough . . . . to permit similar reactions to the same stimuli," and, second, "That the environment is the activating factor in bringing out the potentialities of the subjects for similar development." Typographically the book is well set up; the illustrations are well chosen; there is a section of references for further reading, and an index.

THE ENERGIES OF MEN. *A Study of the Fundamentals of Dynamic Psychology.*

By William McDougall. Charles Scribner's Sons, New York. $2.00. $4\frac{7}{8} \times 7\frac{3}{8}$; xii + 395; 1933.

The distinguished author has combined in this book the essential and fundamental theses presented in his two earlier and well known works, *Outline of Psychology* and *Outline of Abnormal Psychology.* This book is an endeavor to present to the student who is just entering the field of psychology a broad outline of the human organism without too much attention to anatomical and neurological details. Such details, the author says, may be postponed until

> The student shall have learnt to conceive and to think about the nature and activity of man in a profitable manner, and, especially, shall have resolutely grappled with the question of the native basis of human personality, its distinguishable factors, their modes of functioning, their growth and differentiation and integration to form the infinitely complex whole.

The author has also added two "novelties." One is a revision of his theory of instincts and intelligence for which he has heretofore been rather sharply criticized, and the other a new treatment of the learning process.

DO YOU SPEAK CHIMPANZEE? *An Introduction to the Study of the Speech of Animals and of Primitive Men.*

By Georg Schwidetzky. E. P. Dutton and Co., New York. $1.75. $4\frac{3}{4} \times 7\frac{1}{4}$; viii + 133; 1932.

In this interesting but not altogether convincing book Mr. Schwidetzky finds that the sounds made by various animals also occur in human speech and argues that the latter is derived from the former. But a word is not merely a sound; it is a sound which symbolizes a certain meaning. If he could show that the meaning of a word might be derived from the situation in which an animal uses the similar sound his argument would carry greater weight. He also concludes that man resulted from the crossing of widely separated types of primates, such as gibbons and baboons, but gives no evidence that such wide crosses would be possible.

FORTY YEARS OF PSYCHIATRY.

By William A. White. Nervous and Mental Disease Publishing Co., Washington and New York. $3.00. 6×9; v + 154; 1933.

An attempt to trace the changes that have taken place in the attitude toward, and treatment of the mentally sick during the last half century. There is a certain amount of autobiographical material interwoven in the narrative but the author has introduced it only as it bears on his views on psychiatry. The book embodies the ripe wisdom of one who has had long and extensive first-hand experience in dealing with the insane.

SELF-CONSCIOUSNESS AND ITS TREATMENT.

By A. A. Roback. Sci-Art Publishers, Cambridge. $1.50 net. $5\frac{3}{8} \times 8$; 122; 1933.

In this little book, written especially for the members of the Society for Adult Education, there is nothing that the average reader cannot easily comprehend. It treats of the symptoms of self-consciousness, the types of people who are self-conscious, the causes and treatment of self-consciousness, etc. etc. A brief bibliography is given and a series of 100 questions by which the reader can test his knowledge of the text. There is an index.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE NEW BACKGROUND OF SCIENCE.

By Sir James Jeans. The Macmillan Co., New York. $2.50. $5\frac{1}{2} \times 8$; viii + 301; 1933.

After the succession of somersaults which it performed in the earlier decades of the twentieth century, theoretical physics seems to have settled down to a comparatively steady state. In this book Jeans sketches the present situation against a background of rudimentary philosophy, "because I believe, in common with most scientific workers, that without a background of this kind we can neither see our new knowledge as a consistent whole, nor

appreciate its significance to the full." He shows how the view of nature as an assemblage of objects external to oneself, located in space and changing with time, arose; and how modern developments in physics have necessitated a new philosophy whose

essence is that he no longer sees nature as something entirely distinct from himself. Sometimes it is what he himself creates, or selects or abstracts; sometimes it is what he destroys.

In certain of its aspects, which are revealed by the new theory of quanta, nature is something which is destroyed by observation. It is no longer a desert which we explore from the detached position of an aeroplane; we can only explore it by trampling over it, and we raise clouds of dust at every step. Trying to observe the inner workings of an atom is like plucking the wings off a butterfly to see how it flies, or like taking poison to discover the consequences. Each observation destroys the bit of the universe observed, and so supplies knowledge only of a universe which has already become past history.

In certain other aspects, especially its spatio-temporal aspects as revealed by the theory of relativity, nature is like a rainbow. The ancient Hebrew—the analogue of the nineteenth-century physicist—saw the rainbow as an objective structure set in the heavens for all men to behold, the token of a covenant between God and man, and as objective as the signature to a cheque. We now know that the objective rainbow is an illusion. Raindrops break sunlight up into rays of many colours, and the coloured rays which enter any man's eye form the rainbow he sees; but as the rays which enter one man's eyes can never enter those of a second man, no two men can ever see the same rainbow. Each man's rainbow is a selection of his own eyes, a subjective selection from an objective reality which is not a rainbow at all. And it is the same with the nature which each man sees.

As to Heisenberg's celebrated principle of indeterminancy "we can retain *either* the space-time representation of the older pictures *or* the strict determinism, *but never both*." With regard to attempts to press indeterminacy into the service of free-will he is more cautious than some of his confreres. It has always seemed to us that indeterminacy has very little to do with ethics. Moral responsibility depends on the power of conscious choice between alternative acts conceived as good and bad. A person who could act only at random would be as little a free moral agent as one whose acts were mechanically determined. In short the caprices of the electron seem to furnish as poor a basis for free-will as does determinism itself.

THE HEROIC AGE OF SCIENCE. *The Conception, Ideals, and Methods of Science Among the Ancient Greeks. Carnegie Institution of Washington Publication No. 442.*

By William A. Heidel. The Williams & Wilkins Co., Baltimore. $2.50. $5\frac{7}{8}$ x 9; vii + 203; 1933.

The purpose of this book has been "to indicate how the Greeks set about the task of laying the foundations of science, rather than to recount their achievements." It is Heidel's thesis that Greek science differs from modern science mainly in the sense that their methods were the cruder ones adapted to preliminary surveys, and particularly to surveys of a broader scope than are commonly made today. He has arranged his book to illustrate their use of the processes of observation and induction, classification, analogy, and experimentation, and to show that their approach was not different in kind from that of present day science. In particular he is out to controvert the doctrine that the Greeks did not experiment. "The main reason, however, for the infrequency of recorded experiments is the studied brevity of exposition affected by Greek scientists. . . . . Conclusions are offered with only occasional citation of supporting evidence." He has collected a great many of such citations, and we venture to say that almost any scientist ought to find his chapter on experimentation interesting, if not provocative. The book is well documented and has an index.

THE COST OF BIOLOGICAL BOOKS IN 1933

By JOHN R. MINER

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IN ACCORDANCE with the usual custom of the QUARTERLY REVIEW OF BIOLOGY the present paper reports on the cost of books which have been reviewed during 1933. The books are classified as to country of origin in the same rubrics as in previous reports. The prices of foreign books are converted into dollars on the basis of the exchange at the time the books were received.

The total number of pages reviewed in 1933 is 104,725, a decrease of 27.6 per cent from 1932 but an increase of 26.8 per cent over 1926.

As may be seen from Table 2 the general trend of the average prices per page of the biological books reviewed has been downward from 1932 to 1933. Combining all the books reviewed in 1933 the average price per page was 1.005 cents, a decrease of 3.6 per cent from 1932 and of 8.4 per cent from 1926. This is in line with the international decline in general price levels, but, as already noted in the report for 1932, biological books do not seem to have kept pace with other goods in their rate of decline. Thus the books published in the United States show a decrease in price of 8.9 per cent from 1926 to 1933, whereas the wholesale commodity price index of the United States Bureau of Labor Statistics declined about 40 per cent in the same period.

French biological books show an increase in price of 23.3 per cent from 1932 to 1933 and have more than doubled in price since 1926. In all previous years since 1926 French books have been less expensive than any other group of commercially produced scientific books, but in 1933 they are 12 per cent more expensive than English books, which cost less than three-quarters as much as in 1932 and little more than half as much as in 1926. Although the decline in price of English books between 1931 and 1932 probably reflects the drop in the value of the pound during that period, the continued decline in price from 1932 to 1933 cannot be attributed to the same cause, since the pound was stabilized at about 70 per cent of its former value at the beginning of 1932, and varied little in terms of the dollar until the depreciation of the latter in 1933 caused it to rise again. Biological books published in the United States have changed little in price either from 1932 to 1933 or since 1926.

In spite of a decline in price of 10.6 per cent from 1932 to 1933, German books are still the most expensive of any of

TABLE 1

Prices of biological books, 1933

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
German	11,221	$160.15	1.43
British Government	839	11.66	1.39
English-American	9,236	119.45	1.29
United States	59,181	605.80	1.02
Other Countries	2,742	23.41	0.85
France	7,131	52.50	0.74
England	11,426	74.88	0.66
U. S. Government	2,949	4.90	0.17

the groups. The high cost of German medical and scientific publications and especially periodicals bears heavily both on libraries and on individual scientists. A committee of the Medical Library Association, appointed to investigate the situation, found, according to a letter by Eileen R. Cunningham, Chairman of the committee, published in *Science* (Vol. 77, pp. 409–410, 1933), that "in a large or medium-sized library in this country, two thirds or even more of the total annual appropriation for current periodicals is expended on German periodicals, issued chiefly by one or two firms, leaving less than one third of the funds available to be used for the scientific output of all other nations, including the United States and many of the more reasonably priced German publications." The cost of some of these journals has now reached as high as $90.00 to $173.00 a year and, as no definite yearly subscription price is announced, the subscriber cannot know beforehand what he will be called upon to pay. Upon the recommendation of the committee the Medical Library Association has passed the following resolutions (*Science*, Vol. 78, pp. 139–140, 1933):

1. It is recommended that no library subscribe to any periodicals that do not have a fixed annual subscription price for the entire annual output of volumes or parts. That such price be stated in advance, and also a statement of the number and parts to be issued per year.

2. That the Committee on the Cost of Current Medical Periodicals be empowered to invite the various library groups of this and other countries to coöperate with us in the above-mentioned and other measures, necessary to establish more equitable prices for medical and other scientific journals, and that the approach to library organizations in other countries be made first through the president of the International Federation of Library Associations.

3. We believe there is a wide-spread opinion that there must be a substantial reduction in extent of, and in subscription prices for, the most expensive medical and other scientific periodicals, and we further recommend that, unless definite word to this effect is received sufficiently prior to renewal of subscriptions for 1934, libraries cancel their subscriptions to the most expensive journals, except one library in each of 6 to 10 zones throughout the United States and Canada.

TABLE 2

Comparison of the prices of biological books from 1926 to 1933

ORIGIN	AVERAGE PRICE PER PAGE								CHANGE + OR − FROM 1932 TO 1933		CHANGE + OR − FROM 1926 TO 1933	
	1926	1927	1928	1929	1930	1931	1932	1933	Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
English-American	1.55	1.39	1.46	1.90	1.91	2.27	1.48	1.29	−0.19	−12.8	−0.26	−16.8
Other countries	1.51	0.78	1.13*	1.68	0 97	1.53	1.02	0.85	−0.17	−16.7	−0.66	−43.7
England	1.28	1.14	1 09	1.29	1 13	1.19	0.89	0.66	−0 23	−25.8	−0 62	−48.4
United States	1 12	1 09	1.14	1.14	1 09	1.05	1.00	1.02	+0.02	+2.0	−0 10	−8.9
Germany	1 09	1.20	1.48	1.65	1.82	1.75	1.60	1.43	−0.17	−10.6	+0.34	+31.2
British Government		0.96	1 26	0.39	1.19	1.03	1.45	1.39	−0.06	−4 3	+0.43†	+44.8†
France	0.35	0.36	0 45	0.47	0.47	0.69	0.60	0.74	+0.14	+23.3	+0 39	+111.4
U. S. Government	0.31	0.24	0.21	0.23	0.30	0 28	0.36	0.17	−0.19	−52.8	−0.14	−45.2

* With two special treatises omitted as explained in Vol. III, p. 601.

† Change from 1927 to 1933.

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